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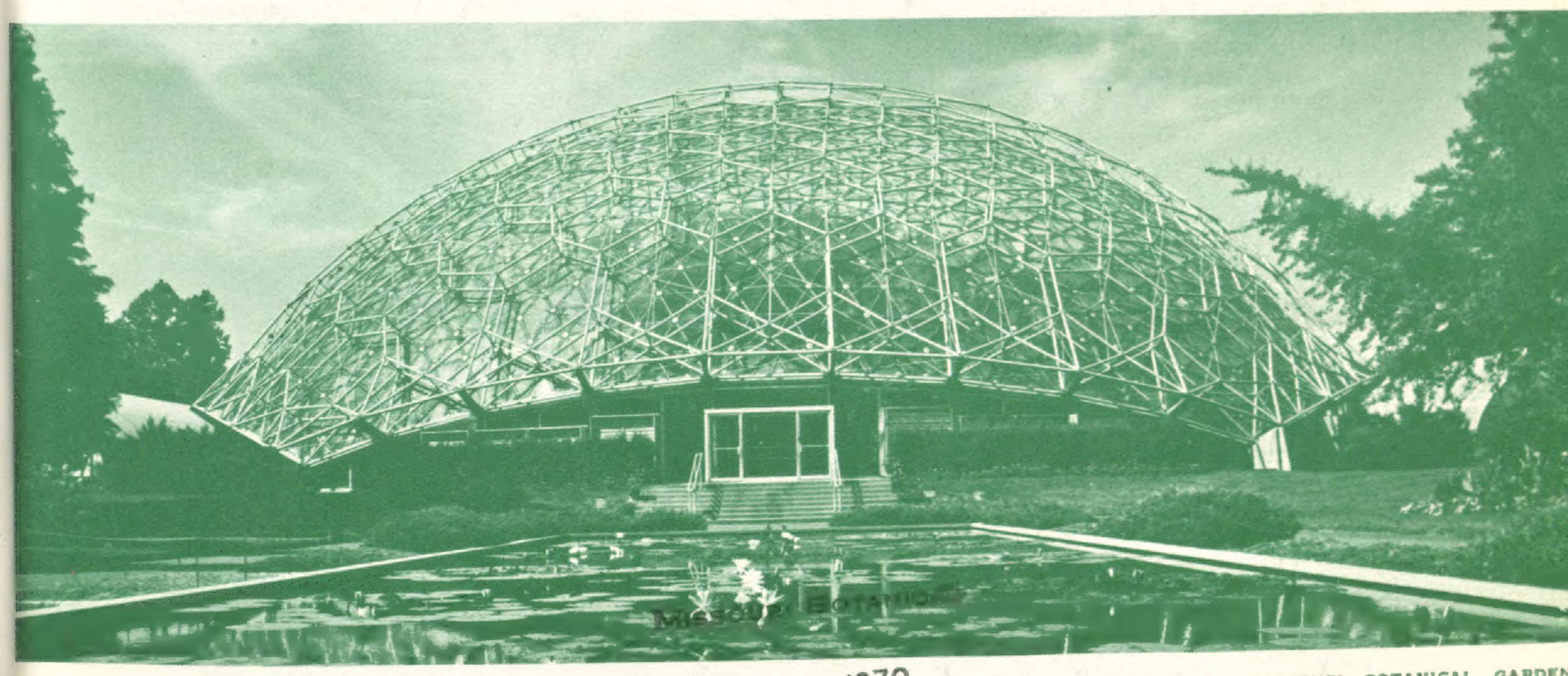

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EVOLUTION, CYTOLOGY AND SUBGENERIC CLASSIFICATION IN *MORAEA* (IRIDACEAE)[1]

PETER GOLDBLATT[2]

ABSTRACT

Moraea, an African genus widespread south of the Sahara, comprising ca. 92 species, is divided into five subgenera: *Moraea*, *Monocephalae*, *Visciramosa*, *Grandiflora*, and *Vieusseuxia*, and into several sections. Chromosome numbers of $n = 10$, 9, 8, 6, 20, and 12 are reported in the 52 species studied to date. A base number of $x = 10$ is postulated for *Moraea*, and *Dietes* is suggested as the closest living ancestor. *Moraea* is pictured as having evolved in the mid to late Tertiary in central southern Africa in response to the onset of a dry climatic regime bordering the tropics. The great radiation of the genus in the southwestern Cape is seen as a more recent phenomenon resulting from the development of a Mediterranean climate in this area. Several nomenclatural changes are made and four new species are described.

The problem of infrageneric classification in *Moraea* was only briefly mentioned in my recent survey of the chromosome cytology of the southern African Iridaceae (Goldblatt, 1971a). In this work the karyotypes of several species were described and discussed with reference to the evolution of the genus, and although only a comparatively small number of species were studied, the cytological evidence was found to be at odds in many instances with existing subgeneric treatments. Thus it was clear that further cytological investigation would provide invaluable information for taxonomic and evolutionary studies and that it would be especially useful at infrageneric levels.

In preparation for a revision of the South African representatives of *Moraea*, which comprise the great majority of the species in the genus, I have undertaken a more extensive karyotypic study. Chromosomal data are now known for 52 species, approximately 70% of the genus, and this information has assisted considerably in evaluating the systematics of *Moraea* because of the strong correlations with certain morphological traits. The comparison of morphology and

[1] This study was supported by a travel grant from the Council for Scientific and Industrial Research of South Africa, and by Grant BMS 74-18905 from the National Science Foundation of the U.S.A.

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cytology has resulted in a complete rearrangement of the classification of Baker (1896), the most recent and only detailed treatment of the genus, and has made possible new interpretations of species relationships. The system presented here was first developed in a revision of the South African species in the summer rainfall area (Goldblatt, 1973), but was necessarily incomplete because of the limited occurrence of *Moraea* in this area. Moreover, no formal ranks between genus and species were recognized in this revision so that the subgeneric treatment is essentially new in the present work.

The cytological data are presented in the first section of the paper as these are central to the revised generic classification. The classification itself is then summarized, followed by an analysis of the karyology and by a phytogeographic and phylogenetic discussion. Finally, four new species are described and several necessary nomenclatural changes are explained.

CHROMOSOME CYTOLOGY

METHOD

The paraffin section method described earlier (Goldblatt, 1971a), was abandoned in favor of a rapid squash technique. Root tips from sprouting corms or germinating seeds were pretreated for three to four hours in 0.05% aqueous colchicine, fixed for two minutes in acetic ethanol 1:3, hydrolyzed in 10% HCl for five minutes at 60° C and squashed in lacto-propionic orcein (Dyer, 1963). This method yielded excellent preparations in the minimum time, and although slides could not readily be made permanent, they kept well for two to three days allowing adequate time for study.

OBSERVATIONS

The outstanding feature that emerges from the cytological survey of *Moraea* (Table 1) is the predominance of species with chromosome numbers based on either $x = 10$ ($2n = 20, 40$) and $x = 6$ ($2n = 12, 24, 36$); the few exceptions to this so far discovered are *M. papilionacea*, $2n = 18$, *M. fugax* in which $2n = 20$, 16 and 12 occur, and only one of the several populations of *M. ciliata* examined, also $2n = 18$ (Table 1). *Moraea papilionacea* is clearly allied to the group of species with $x = 10$ and must be regarded as an aneuploid species and not, as might appear, a triploid based on $x = 6$. The existence of a $2n = 18$ population in *M. ciliata* (predominantly $2n = 20$), requires more detailed study as its significance is not yet known, but as *M. ciliata* is also related to other species with $2n = 20$, the $2n = 18$ is clearly derived.

The situation in *M. fugax*, in which the three populations studied have quite different numbers, $n = 10$, 8 and 6, is more complex. The immediate impression is that this species, if in fact it is only one species, is the link between the two main chromosome groups, which are based on $x = 10$ and $x = 6$. This interpretation does not seem correct simply on morphological grounds, since *M. fugax* has a very distinctive morphology which suggests it is not a direct ancestor of the large and heterogeneous group with $x = 6$.

TABLE 1. Chromosome numbers in *Moraea*. The following abbreviations are used: C.P. = Cape Province; Tvl. = Transvaal; S.W.A. = South West Africa.

Species	Diploid Chromosome Number	Collection Data or Reference to Previous Work
	Subg. *MORAEA*	
	Sect. *Moraea*	
M. fergusoniae L. Bol.	20	C.P.: Robinson Pass, *Heimstra s.n.* (MO). Botrivier-Villiersdorp, *Goldblatt 216* (BOL).
M. gawleri Spreng.	20	C.P.: Cape Point Res., (Goldblatt, 1971a).
	24	C.P.: Van Rhyns Pass, *Goldblatt 223* (J).
M. lugubris (Salisb.) Goldbl.	20	C.P.: Southern Cape Peninsula, *Goldblatt*, no voucher.
M. margaretae Goldbl.	40	C.P.: Near Nababeep, *Goldblatt 628* (BOL). Flats E of Nababeep, *Goldblatt 3061* (MO).
M. papilionacea (L.f.) Ker	18	C.P.: Tulbagh Road, (Goldblatt, 1971a). Constantia Nek, (Goldblatt, 1971a). Kenilworth flats, *Goldblatt*, no voucher.
M. ramosissima (L.f.) Druce	20	C.P.: Stellenbosch, (Goldblatt, 1971a) (Sakai, 1952).
M. serpentina Baker (or as *M. framesii* L. Bol.)	20	C.P.: Springbok, *Goldblatt 626* (BOL). Van Rhyns Pass, (Goldblatt, 1971a). Slopes W of Springbok, *Goldblatt 3043* (MO). 40 km S of Springbok, *Goldblatt 3041* (MO).
M. vegeta L. (as *M. juncea*)	20	C.P.: Groot Constantia, (Goldblatt, 1971a). (Fernandes & Neves, 1961).
	Sect. *Deserticola*	
M. bolusii Baker	20	C.P.: Between Steinkopf and Okiep, *Goldblatt 2772* (MO).
	Sect. *Acaules*	
M. ciliata (L.f.) Ker	20	C.P.: Nieuwoudtville, (Goldblatt, 1971a). Verlate Kloof, Sutherland, *Goldblatt 548* (BOL). Koedoes Mts., *Goldblatt*, no voucher.
	20, 18	C.P.: Glenlyon, Nieuwoudtville, *Strauss s.n.* (NBG 90218).
	18	C.P.: Darling-Mamre road, *Goldblatt*, no voucher.
	40	C.P.: Between Queen Anne and Eseljacht, *Goldblatt 2498* (MO).
M. falcifolia Klatt	20	C.P.: Nieuwoudtville, *Goldblatt 564* (BOL). 4 km W of Steinkopf, *Goldblatt*, no voucher.
M. macronyx Lewis	20	C.P.: Calvinia dist., (Goldblatt, 1971a). Near Avontuur, *Goldblatt 2860* (MO).
	Sect. *Subracemosae*	
M. fugax (de la Roche) Jacq. (or as *M. edulis*)	12	C.P.: Hopefield, (Goldblatt, 1971a).
	16	C.P.: 10 km N of Malmesbury, *Goldblatt 3025* (MO).
	28	(Sakai, 1952).
M. fugax var. *gracilis* Baker	20	C.P.: Flats S of Pikenierskloof Pass, *Goldblatt 3279* (MO).
M. filicaulis Baker (as *M. diphylla* Baker)	12	C.P.: Giftberg, *Goldblatt 207* (BOL).

TABLE 1. (continued)

Species	Diploid Chromosome Number	Collection Data or Reference to Previous Work
	Sect. *Tubiflora*	
M. cooperi Baker	20	C.P.: Caledon dist., (Goldblatt, 1971a).
	Subg. *MONOCEPHALAE*	
M. angusta (Thunb.) Ker	20	C.P.: Malmesbury, (Goldblatt, 1971a).
M. cf. *angusta*	20	C.P.: Bainskloof, *Goldblatt*, no voucher.
M. anomala Lewis (as *M. neglecta*)	20	C.P.: Elim, (Goldblatt, 1971a).
M. neglecta Lewis	20	C.P.: Sandy flats E of Hermanus, *Goldblatt* 2999 (MO).
	Subg. *VISCIRAMOSA*	
M. bituminosa (L.f.) Ker	20	C.P.: Hermanus, *Goldblatt* 3325 (MO).
M. elsiae Goldbl.	20	C.P.: Kenilworth Racecourse, *Esterhuysen* 32358 (BOL).
M. odorata Lewis	20	C.P.: Quoin Pt., (Goldblatt, 1971a). Rondebosch Common, *Barnard s.n.* (BOL).
M. "viscaria" (L.f.) Ker	20	C.P.: Giftberg, *Goldblatt* 353 (BOL). Near Elim, *Goldblatt*, no voucher.
	Subg. *VIEUSSEUXIA*	
	Sect. *Polyanthes*	
M. carsonii Baker	12	Zambia: Kandalila Falls, *Strid 2900* (C).
M. elliotii Baker (or as *M. setacea*)	12	(Lewis, 1966). C.P.: 15 km S of Grahamstown, *Goldblatt 2864* (MO).
	24	C.P.: Fort Hare, *Goldblatt 455* (BOL).
M. erici-rosenii Fries	12	(Lewis, 1966).
M. polyanthos L.f.	12	C.P.: Ladismith, *Goldblatt 661* (BOL). Oudtshoorn campsite, *Goldblatt 2922* (MO).
M. polystachya (L.f.) Ker	12	C.P.: Beaufort West, (Goldblatt, 1971a). Graaff Reinet, (Goldblatt, 1971a). 10 km W of Grahamstown, *Goldblatt*, no voucher. S.W.A.: Huns Mts., *Tolken* 3985 (BOL). (Riley, 1962).
M. stricta Baker (as *M. trita*)	24	Tvl.: Johannesburg, *Goldblatt*, no voucher.
	36	Tvl.: Haenertsburg, *Goldblatt*, no voucher.
	Sect. *Vieusseuxia*	
M. algoensis Goldbl.	12	C.P.: Wildehondekloof Pass, *Goldblatt 2840* (MO).
M. aristata (de la Roche) Asch. & Graeb.	12	C.P.: Observatory grounds, Cape Town, *Goldblatt 1299* (MO).
M. barnardii L. Bol.	12	C.P.: Shaws Pass, *Strauss 35* (NBG).
M. bellendenii (Sweet) N.E.Br.	12	C.P.: Napier, (Goldblatt, 1971a).
M. caeca Goldbl.	12	C.P.: Dasklip Pass, *Goldblatt 678* (BOL).
M. debilis Goldbl.	12	C.P.: Caledon dist., *Goldblatt 673* (BOL).
M. gigandra L. Bol.	12	Ex hort., *Goldblatt*, no voucher.
M. insolens Goldbl.	12	C.P.: Drayton, Caledon, (Goldblatt, 1971a).
M. loubseri Goldbl., ined.	12	C.P.: Langebaan, *Loubser 2228* (NBG).
M. lurida Ker	12	C.P.: Klein Hagelkraal, (Goldblatt, 1971a). Hermanus, *Goldblatt 3311* (MO). Houw Hoek Pass, *Goldblatt*, no voucher.

TABLE 1. (continued)

Species	Diploid Chromosome Number	Collection Data or Reference to Previous Work
M. neopavonia Foster	12	C.P.: Heuningberg, *Goldblatt 655* (BOL).
M. tenuis Ker	12	C.P.: Brandvlei, *Goldblatt 587* (BOL). Steinkopf, *Goldblatt 2777* (MO). Hills above Hermanus, *Goldblatt 3010* (MO).
M. thomasiae Goldbl.	12	C.P.: Burgher's Pass, Koo, *Thomas s.n.* (BOL).
M. tricuspidata (L.f.) Lewis	24	C.P.: Jeffreys Bay, *Goldblatt 2893* (MO).
	12	C.P.: Kirstenbosch hill, Cape Peninsula, *Goldblatt*, no voucher.
M. tripetala (L.f.) Ker	12	C.P.: Nieuwoudtville, (Goldblatt, 1971a). Ceres, *Goldblatt 667* (BOL). Koedoes Mts., *Goldblatt 547* (BOL).
M. tulbaghensis L. Bol.	24	C.P.: Gouda Common, *Goldblatt*, no voucher.
M. villosa Ker	24	C.P.: Tulbagh, (Goldblatt, 1971a). Riebeeck Kasteel, (Goldblatt, 1971a).
		Subg. *GRANDIFLORA*
M. alticola Goldbl.	12	Natal: Drakensberg, *Trauseld* s.n. (BOL).
M. graminicola Oberm. subsp. *graminicola*	12	Natal: Mooi River, (Goldblatt, 1971a).
M. huttonii (Baker) Oberm.	12	Natal: Nottingham, *Moll 2666* (PRE).
M. macrantha Baker	12	Malawi: *Pawek 6966* (K, MO).
M. moggii N.E.Br. subsp. *moggii*	12	Tvl.: Lochiel, (Goldblatt, 1971a).
M. schimperi (Hochst) Pichi-Serm	12	Malawi: Nyika, (Goldblatt, 1971a). Livingstonia dist., *Goldblatt 15* (J).
M. spathulata (L.f.) Klatt subsp. *spathulata*	12	C.P.: Knysna, (Goldblatt, 1971a). O.F.S.: Harrismith, (Goldblatt, 1971a).
subsp. *transvaalensis* Goldbl.	12	Tvl.: Graskop, (Goldblatt, 1971a).
subsp. unknown	12	(Riley, 1962).

Even with the three exceptional species in which base numbers other than $x = 10$ and $x = 6$ occur, the difference between the two main groups appears remarkable and it is unlikely with about 70% of the genus known cytologically that more species will be found linking these groups, especially as most of those unknown chromosomally are specialized and closely allied to species with $x = 6$.

Species such as *M. stricta* ($2n = 24, 36$), *M. villosa*, and *M. tulbaghensis* (both $2n = 24$) are clearly polyploid and not aneuploids derived from $2n = 20$. This is clear both because the species closely related to these polyploids have diploid numbers of $2n = 12$, and equally from considerations of chromosome length where the polyploid does in fact have approximately twice the amount of chromosome material compared with plants having $2n = 12$ or $2n = 20$ (Table 2).

The occurrence of $2n = 20$ in one population (several individuals of *M. gawleri*), while a second (only 2 specimens) has $2n = 24$ is curious. This species clearly belongs to the $2n = 20$ group and the anomalous record of $2n = 24$ may

TABLE 2. Chromosome size in several species of *Moraea*.

Species	Diploid Number $2n$	Haploid Chromosome Length μ
M. falcifolia Klatt	20	54
M. lugubris (Salisb.) Goldbl.	20	49.5
M. cf. *viscaria* (L.f.) Ker	20	68
M. angusta (L.f.) Ker	20	56.5
M. barnardii L. Bol.	12	57
M. tenuis Ker	12	61.5
M. alticola Goldbl.	12	67.5
M. thomasiae Goldbl.	12	61
M. tulbaghensis L. Bol.	24	114

be due to the presence of B chromosomes. Unfortunately, due to difficulties in growing this species, no more information is available.

While most species each has a characteristic karyotype, notable variations occur within forms of *Moraea tripetala*, particularly in the size, shape, and location of the satellite. In a few other species heteroploidy has been recorded. Variations in ploidy levels occur in *M. ciliata*, *M. elliotii*, and *M. tricuspidata* all of which have both diploid and tetraploid populations, while *M. stricta* evidently has both tetraploid and hexaploid populations. Aneuploid differences occur in *M. ciliata* with most populations $n = 10$ but $n = 9$ in one population and in *M. fugax* where *M. fugax* var. *fugax* has $n = 8$ and 6 while var. *gracilis* has $n = 10$. All these examples of intraspecific variation in chromosome number require more detailed study and will undoubtedly have significance at the species level. For the purposes of interpreting subgeneric and interspecific relationships, heteroploidy is less important and may safely be disregarded, except in *M. fugax* which will be discussed further.

Because the chromosomes are quite large in *Moraea*, ranging from about 4–8 μ in the $x = 6$ group and from 2–5 μ in the $x = 10$ group with the method described here, considerable detail of the karyotype can be seen (Figs. 1–2). Relative length of chromosomes and the position of the centromeres and satellites all contribute to greater understanding of species relationships. The size and position of the satellite are particularly useful features in indicating small natural groups. Details of karyotype relating to classification are discussed in the following pages.

SUBGENERIC CLASSIFICATION

SYNOPSIS OF TREATMENT

Subg. 1. **Moraea** $x = 10$

Plants simple to many branched. Leaves (1–)2–many. Bracts and spathes usually acute. Corm tunics pale to black, never sticky. Outer tepals reflexed, inner either erect or spreading to reflexed. Seeds small and ± spherical-angled.

Type species: *M. vegeta* L. Species: ca. 21

Distribution: Cape Province, from Cape Town north to the Orange River and east to Kimberley and Grahamstown.

Sect. 1. *Moraea*

Plants few to many branched. Leaves (2–)3–many. Stem erect, produced above ground.

Type species: *M. vegeta* L. Species: ca. 10

Distribution: Cape Province, from Cape Town north to the Orange River and east to Kimberley and Humansdorp.

Sect. 2. *Acaules* Baker

Plants simple or branched. Leaves several. Stems entirely subterranean.

Type species: *M. ciliata* (L.f.) Ker Species: ca. 4

Distribution: Cape Province, from Cape Town north to Namaqualand and east to Graaf Rienett and Grahamstown.

Sect. 3. *Deserticola* Goldbl.[3]

Plants simple or few to many branched. Leaves solitary. Stems well developed.

Type species: *M. bolusii* Baker Species: ca. 4

Distribution: Dry areas of the northwestern Cape, from the van Rhynsdorp district in the south to southern South West Africa.

Sect. 4. *Subracemosae* Baker

Plants few to many branched. Leaves 1 or 2, with leaf inserted well above ground at base of inflorescence. Stem well developed. Capsule strongly beaked.

Type species: *M. fugax* (de la Roche) Jacq. (lectotype) Species: 2

Distribution: Namaqualand to southwestern Cape.

Sect. 5. *Tubiflora* Goldbl.[4]

Plants much branched. Leaves 2–3. Flowers solitary in spathes, with a true perianth tube and inner tepals lacking.

Type species: *M. cooperi* Baker Species: 1

Distribution: Southwestern Cape.

Subg. 2. **Monocephalae** (Baker) Goldbl., stat. nov.

Monocephalae Baker, Fl. Cap. 6: 10. 1896, basionym (sect.). $x = 10$

Plants unbranched. Leaf solitary, terete. Stem well developed, nodes often viscous. Bracts usually obtuse. Seeds flattened, platelike.

Type species: *M. angusta* (Thunb.) Ker (lectotype) Species: 3

Distribution: Southwestern and southern Cape as far east as George.

Subg. 3. **Visciramosa** Goldbl.[5] $x = 10$

Plants several to many branched, conspicuously viscous below the nodes. Produced leaves 2. Corm tunics pale to dark brown and oily on inner surfaces. Tepals spreading to reflexed. Seeds angled.

Type species: *M. bituminosa* (L.f.) Ker Species: ca. 4

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[3] Sect. *Deserticola* Goldbl., sect. nov. Planta simplex ad multiramosa. Folium solitarium. Caulis producta. Typus: *M. bolusii* Baker.

[4] Sect. *Tubiflora* Goldbl., sect. nov. Planta multiramosa. Folia 2–3. Flores solitarii in spathae; tubus perianthii productus; tepala interiora absentia. Typus: *M. cooperi* Baker.

[5] Subg. *Visciramosa* Goldbl., subg. nov. Planta multiramosa, viscosa subnodos. Folia 2. Tunicae cormi pallidi brunneae, oleosae in pagina inferiora. Tepala effusa ad reflexa. Semina angulata. Typus: *M. bituminosa* (L.f.) Ker.

Distribution: Cape Province, from Cape Town north to Namaqualand and east to Grahamstown.

Subg. 4. **Vieusseuxia** (de la Roche) Baker $x = 6$

Plants simple to many branched. Leaves usually solitary or 3–5. Stems well developed. Bracts and spathes acute. Seeds angled or with ± spongy testa.

Type species: *M. bellendenii* (Sweet) N.E. Br. (lectotype) Species: ca. 35
Distribution: South Africa to Ethiopia.

Sect. 6. *Polyanthes* Goldbl.[6]

Plants few to many branched. Leaves 1–5, usually solitary. Inner tepals entire, well developed. Seeds angled.

Type species: *M. polystachya* (L.f.) Ker Species: ca. 10
Distribution: Ethiopia to the southwestern Cape.

Sect. 7. *Vieusseuxia*

Plants simple or few branched. Leaf solitary (rarely 2). Flowers much modified, inner tepals usually trifid or much reduced to absent. Seeds angled or with ± spongy testa.

Type species: *M. bellendenii* (Sweet) N.E. Br. Species: ca. 25
Distribution: South Africa, Transvaal to southwestern Cape.

Subg. 5. **Grandiflora** Goldbl.[7] $x = 6$

Plants unbranched, usually large. Produced leaf solitary. Flowers with inner tepals entire and erect. Seeds depressed, triangulate to discoid.

Type species: *M. spathulata* (L.f.) Klatt Species: ca. 16
Distribution: Ethiopia to South Africa (excluding southwestern Cape).

DISCUSSION

Chromosome number has been a major factor in establishing natural species groups and, as a result, in influencing the subgeneric classification. Consideration of cytological data together with morphology has resulted in the placing of species with $x = 10$ (9) and including *M. fugax* with $x = 10$, 8 and 6 in three subgenera: *Moraea*, *Monocephalae* and *Visciramosa*; while species with $x = 6$ were segregated in two subgenera: *Vieusseuxia* and *Grandiflora* (Fig. 3).

As thus subdivided, each subgenus is believed to constitute a natural assemblage of species with a common ancestor. The base number of $x = 10$ is regarded as ancestral in the genus and the three subgenera with this number are probably best regarded as of great age and, while themselves natural groups, have diverged from one another to such a degree that they cannot be reasonably accommodated in a single subgenus without also including the subgenera with $x = 6$.

The species with $x = 6$ are treated as comprising the two subgenera *Vieusseuxia* and *Grandiflora*. Since they are very distinct morphologically, they are, in my

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[6] Sect. *Polyanthes* Goldbl., sect. nov. Planta pauci- ad multiramosa. Folia 1–5. Tepala interiora integra, producta. Semina angulata. Typus: *M. polystachya* (L.f.) Ker.

[7] Subg. *Grandiflora* Goldbl., subg. nov. Planta simplices. Folium solitarium. Flores generales; tepala interiora integra, erecta. Semina depressa, triangulata ad discoidea. Typus: *M. spathulata* (L.f.) Klatt.

opinion, unlikely to have evolved in a single evolutionary line from the basic stock with $x = 10$. Thus the chromosome number of $2n = 12$ is believed to have evolved independently, at least three times, in subg. *Vieusseuxia*, subg. *Grandiflora*, and *M. fugax* (subg. *Moraea*).

Subg. 1. Moraea.—This subgenus is morphologically heterogeneous and is here divided into five sections. Section *Moraea* comprises several quite unspecialized species having from 2 to many produced leaves, usually a well developed branching system (occasionally simple in depauperate specimens) and generalized flowers with entire, ± spreading inner tepals. This type of flower is also found in the three species of sect. *Acaules* but here the plant itself is greatly modified with a reduced aerial stem—only the upper part of the leaves and the inflorescence emerge above ground level. While the axis is still branched in *M. falcifolia*, the other species of sect. *Acaules*, *M. ciliata* and *M. macronyx*, are more reduced and are unbranched.

The karyotypes of sect. *Moraea* and sect. *Acaules* are, with the exception of *M. papilionacea* ($2n = 18$), strikingly similar: there are usually 3–4 pairs (occasionally 5) of long chromosomes and a corresponding number of much smaller pairs. The satellites are usually large and located on a small chromosome pair (Figs. 1B–D). *Moraea vegeta* and *M. papilionacea* (Goldblatt, 1971a: 345–346) are exceptions with satellites on long chromosomes, and this may be indicative of a natural relationship as they are morphologically quite similar. In *M. ciliata* and *M. macronyx* there are a second pair of satellites on long chromosomes as well as the pair on short chromosomes.

The affinities of sect. *Deserticola*, unusual in subg. *Moraea* in having a solitary leaf, are clearly with species such as *M. serpentina* of sect. *Moraea* and the karyotype of *M. bolusii* (Fig. 1E) is almost identical with that of *M. serpentina* (Fig. 1D); the chromosome complement is distinctive in comprising three long, two medium long and five small chromosome pairs. The asymmetrical corm with its black, fibrous tunics of species of sect. *Deserticola* is very like those of *M. serpentina* and their relationship is very close; in fact, the presence of the single leaf was the only factor in deciding on sectional status for this small alliance.

Moraea fugax in which chromosome numbers of $n = 10$, 8, and 6 have been recorded, as well as the dubious $2n = 28$ by Sakai (1952), is placed together with the closely related *M. filicaulis* in sect. *Subracemosae* of subg. *Moraea*. The placement in this group may appear inconsistent since the base number in subg. *Moraea* is $x = 10$, while lower base numbers predominate in sect. *Subracemosae*. The decision was influenced primarily by the nature of the karyotype in *M. fugax* var. *gracilis*, which has $n = 10$; the karyotype matches exactly those found in sect. *Moraea*, and comprises six long acrocentric chromosomes and seven much shorter pairs (Fig. 1F). *Moraea fugax* var. *gracilis* appears, from the morphological point of view, ancestral to other forms of *M. fugax*, as well as *M. filicaulis*, as it is a large much branched plant in contrast with the smaller, fewer branched forms with lower chromosome numbers. In other respects it is similar to var. *fugax* and *M. filicaulis*, having in common with these the peculiar leaf insertion high up on the stem and the beaked ovary, unique to this group. A critical survey of the cytology of the heteroploid and also morphologically variable *M. fugax* seems

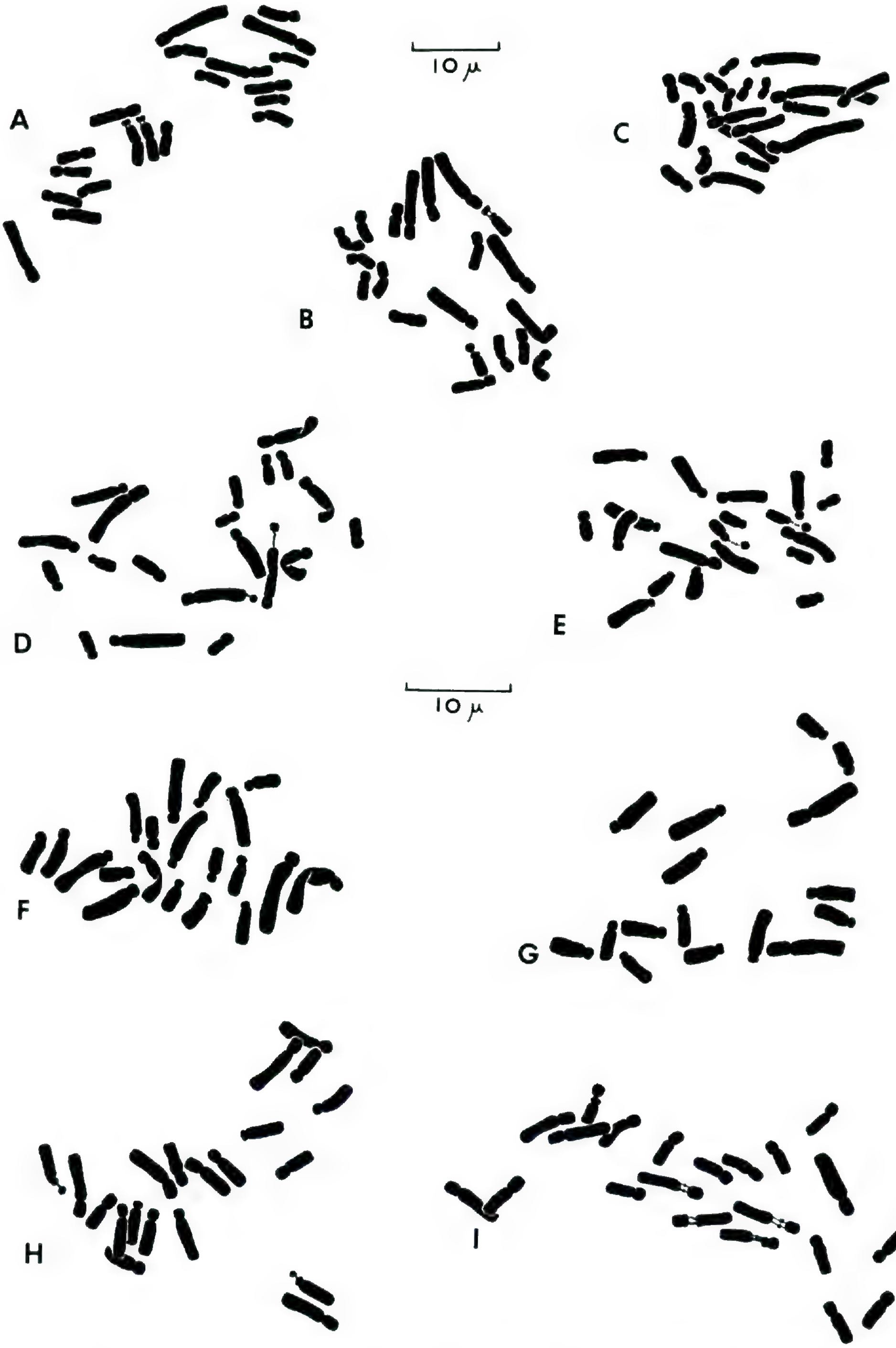

Figure 1. Karyotypes in *Moraea* subgenera *Moraea*, *Visciramosa*, and *Monocephalae*.—A. *M. cooperi*.—B. *M. lugubris*.—C. *M. falcifolia*.—D. *M. serpentina*.—E. *M. bolusii*.—F. *M. fugax* var. *gracilis*.—G. *M. fugax* var. *fugax*.—H. *M. angusta* (s.l.).—I. *M. elsiae*. [Upper scale applies to A–C, H–I; lower to D–G.]

called for and species limits will almost certainly be redefined in the light of further cytological and morphological study.

Section *Tubiflora*, comprising only one species, *M. cooperi*, resembles sect. *Moraea* vegetatively in having a ramified axis. Its flowers are, however, unique in the genus, having a true perianth tube; the flowers are also unusual in being solitary in each inflorescence spathe and in lacking inner tepals. Unusual as *M. cooperi* is, the karyotype is like those found in sect. *Moraea* in having long pairs and large satellites on one of the seven short pairs of chromosomes (Fig. 1A).

Subg. 2. Monocephalae.—Subgenus *Monocephalae* is small, comprising *Moraea angusta* and the two species *M. neglecta* and *M. anomala* segregated by Lewis (1949). Lewis's treatment is followed here with reservation, as the species of the section require critical morphological study. Species in subg. *Monocephalae* have a very distinctive morphology with a simple stem and a solitary terete leaf, but the flowers are unspecialized, large and usually yellow. Without cytological data, the affinities of the species in this section would have remained misunderstood, for the general morphological reduction, large generalized flowers, and the flattened seeds are strongly reminiscent of subg. *Grandiflora* and these two subgenera were in fact regarded as a single section by Baker in his treatment. Other features, such as the somewhat obtuse bracts and spathes, and the sticky exudate below the nodes in some forms suggest affinity with subg. *Visciramosa*. While the chromosome number of $2n = 20$ (Fig. 1H) places subg. *Monocephalae* close to subg. *Moraea*, the karyotypes are not particularly alike and size differences between the chromosomes are not at all distinct. The similarities of subg. *Monocephalae* to subg. *Grandiflora* are believed to be independently derived, and *M. angusta* and its two allies probably evolved in parallel fashion with subg. *Grandiflora* to achieve the reduction of branching and leaf number while retaining an ancestral chromosome number.

Subg. 3. Visciramosa.—This remarkable group stands in a somewhat isolated position. The ± 4 species, which are characterized by a highly ramified inflorescence, curiously sticky patches on the stem below each node, a distinctive corm with brown tunics covered by an oily secretion, and flowers with broad, spreading to strongly reflexed segments and occasionally free stamens, give no particular indication of relationships to other groups within the genus. The chromosomes of the three species studied are similar and the karyotype of only one species, *M. elsiae*, is illustrated (Fig. 1I). There are no sharp size differences amongst the chromosomes, though 2 to 3 larger pairs occasionally stand out; a distinguishing feature of the karyotype is the characteristically small satellite found on a small chromosome pair. This satellite location is frequent though not invariable in the $x = 10$ group.

Subg. 4. Vieusseuxia.—Although subg. *Vieusseuxia* is by far the largest subgenus with ± 35 species, about 40% of the genus, it is morphologically more uniform in vegetative habit than the $x = 10$ group, though the flower is much more varied. With the exception of *M. polystachya*, *M. polyanthos*, *M. carsonii*, its close allies, and a peculiar form of *M. tripetala*, all species have a single produced leaf and relatively few or no branches. In contrast to the vegetative uniformity, the flowers of many species have become specialized in remarkable ways.

Many natural species groups can be recognized in this subgenus but only two major groups are given recognition as sections. The least specialized species are placed in sect. *Polyanthes* with *Moraea polystachya* and its allies. They include forms with a much branched axis and 3–5 leaves, as well as more specialized forms with a solitary leaf and fewer branches. The flowers are generally unmodified and are blue. The karyotypes found in this section are perhaps the least specialized of the species with a base number of $x = 6$, in that they are usually fairly symmetrical, an unspecialized karyotypic feature.

Apart from similarities in the karyotypes of closely related species, the karyotypes found in sect. *Polyanthes* are varied and suggest that the section comprises several distantly related entities. A comparison of the karyotypes of *M. polyanthos* (Fig. 2F) with the previously published figure for *M. stricta* (as *M. trita*) (Goldblatt, 1971a: 348) illustrates this contention. Sect. *Polyanthes* is regarded as a link between subg. *Moraea* and sect. *Vieusseuxia* but chromosomal data place it firmly in the latter. In spite of its intermediate position it is not possible to give sect. *Polyanthes* higher rank as species like *M. elliotii* clearly link the group to sect. *Vieusseuxia*, exhibiting strong similarity to *M. algoensis* and *M. tripetala*, and the dividing line between the two sections is almost arbitrary.

Sect. *Vieusseuxia* is characterized by modification and reduction of the inner tepals in most species, exceptions being *Moraea insolens*, and some forms of *M. neopavonia* and *M. lurida*. Typically the inner tepals are small and trifid but many may be quite reduced to short entire cusps or are absent as in *M. barnardii*. The trend to reduction of the inner tepals is not unique and also occurs quite independently in sect. *Moraea* where some forms of *M. fergusoniae* have trifid tepals while in *M. cooperi* they are absent. The section contains several distinct groupings each with characteristic morphology and karyotype.

Moraea tripetala and its allies, such as *M. algoensis*, *M. barnardii*, *M. debilis* and *M. tenuis* (Figs. 2A, B, C), have similar karyotypes, usually with a small satellite on a long chromosome pair. Some variability occurs within species especially in *M. tenuis* and *M. tripetala* where satellites differ in size and position. The so-called peacock moraeas, *M. neopavonia*, *M. villosa*, *M. tulbaghenis*, *M. loubseri*, and *M. caeca* (Figs. 2D, E), characterized by outer tepals with a broadly ovate to circular limb, usually with a bright color and with distinct markings, have a karyotype in which one of the longest chromosome pairs is submetacentric and bears small satellites.

In contrast, *Moraea bellendenii*, *M. lurida*, *M. insolens*, and *M. tricuspidata*, which appear to be closely allied, do not share many karyotypic features. Large satellites are located on long metacentric chromosomes in *M. bellendenii* and *M. insolens*, and are variable in *M. lurida*, being either large and located on a long metacentric pair or on a smaller, acrocentric pair, while in the heteroploid *M. tricuspidata*, the satellites are small.

The karyotype of *Moraea thomasiae* with its acrocentric chromosome complement (Fig. 2G) is rather different from other species in sect. *Vieusseuxia*. This tends to confirm its rather isolated position in the alliance.

Several species in this section occur in the summer rainfall area of South Africa and await cytological examination.

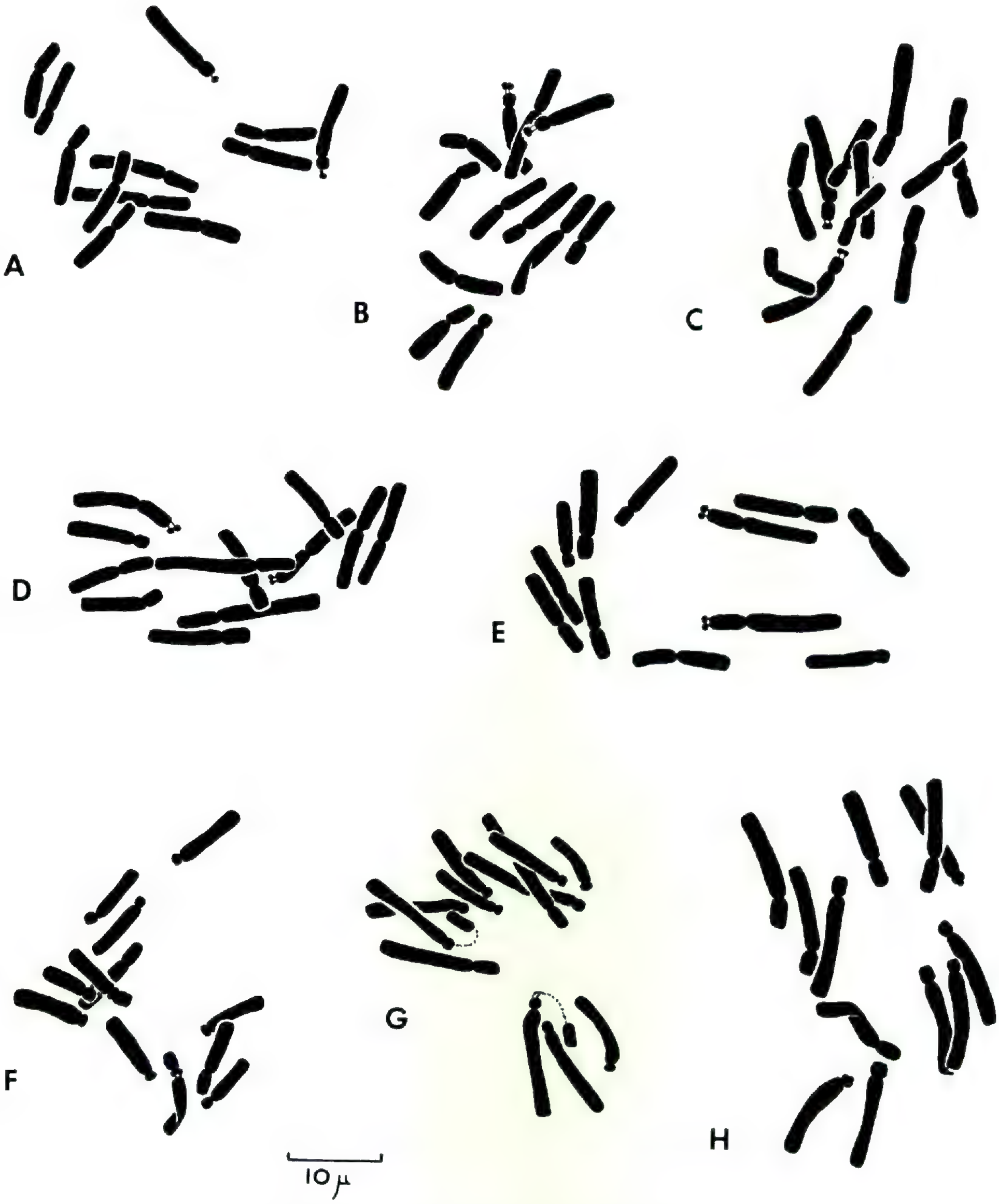

FIGURE 2. Karyotypes in *Moraea* subgenera *Vieusseuxia* and *Grandiflora*.—A. *M. barnardii*.—B. *M. debilis*.—C. *M. tenuis*.—D. *M. caeca*.—E. *M. neopavonia*.—F. *M. polyanthos*.—G. *M thomasiae*.—H. *M. alticola*.

Subg. 5. Grandiflora.—In marked contrast to the previous subgenus, subg. *Grandiflora* is florally uniform and all species have large, usually yellow flowers which have erect inner tepals and spreading outer tepals. Nevertheless the group is believed to be advanced and is very modified in vegetative character. The large produced leaf is always solitary and the branching is entirely reduced (only in the rarest cases are individuals of *M. huttonii*, or *M. spathulata* ever branched). Cytologically the section is very uniform and the karyotype of *M. alticola* (Fig.

2H) is representative of the group; there are two pairs of submetacentric chromosomes, the remaining four are acrocentric to almost telocentric, and a small satellite is present on a long, often apparently telocentric chromosome pair. All too few species of this widespread group are cytologically known and those from tropical Africa especially require investigation. Morphological uniformity however suggests that few cytological surprises are to be expected.

Note on Baker's Classification in Flora Capensis.—Baker's view of *Moraea* was much broader than the one accepted here, as two of his four subgenera, *Dietes* and *Helixyra*, are today regarded as distinct genera, the last mentioned now *Gynandriris*. Baker's remaining two subgenera, *Vieusseuxia* and *Moraea* (as *Eumoraea*), are retained in name only, for the composition and circumscription are entirely altered. Owing to the poorly known state of *Moraea* when Baker worked, his errors are easily understood. In some cases correction of his treatment was only possible with recourse to cytological data. As an example, Baker's *Monocephalae* can be quoted; in this section he included both *M. angusta* ($2n = 20$) and *M. spathulata* ($2n = 12$), as well as two other species not conforming even to his own definition of the section. *Monocephalae*, treated here as a subgenus, is retained in a narrow sense including only *M. angusta* and its two close allies. Wherever possible, Baker's sections are retained, though often redefined so as to conform to the revised system. Thus, when possible, the older treatment is followed or emended and the present system represents a continued refinement initiated by the author (Goldblatt, 1973) through new methods of study.

EVOLUTION

The underlying assumption throughout this paper has been that the $x = 10$ (9) group of species, i.e., subgenera *Moraea*, *Monocephalae*, and *Visciramosa*, comprise the more primitive part of the genus, a hypothesis based primarily on morphological evidence. Most species in subgenera *Moraea* and *Visciramosa* have more than one leaf and numerous branches, a condition believed to be the ancestral growth form in the genus. Though specialized species with a single leaf and with reduced branching are found in the primitive subgenera with $x = 10$, notably the species of subgenus *Monocephalae*, the great majority of the species with this reduced habit, including those with very specialized flowers, have low chromosome numbers, either 8 or predominantly $x = 6$. As indicated earlier, there is reason to believe that the low base number of $x = 6$ was derived independently in at least three lines of evolution (Fig. 3).

The cytological data strongly support the basic assumption that $x = 10$ is the base number for *Moraea*, for as already shown, diploid species with $n = 10$ have approximately the same amount of chromosome material as species with $n = 6$ and cannot therefore be derived by polyploidy and subsequent loss of chromosomes from the latter group. Thus, $x = 6$ is seen as having been derived from an ancestral base number of $x = 10$ by decreasing aneuploidy, and the author's earlier tentative suggestion to this effect (Goldblatt, 1971a: 356) is therefore maintained. One surprising feature, however, is the paucity of intermediates between $x = 10$ and $x = 6$; *Moraea papilionacea* with $n = 9$, a form of *M. ciliata* also with $n = 9$ and *M. fugax* with $n = 10$, 8, and 6 being the only known exceptions. Sub-

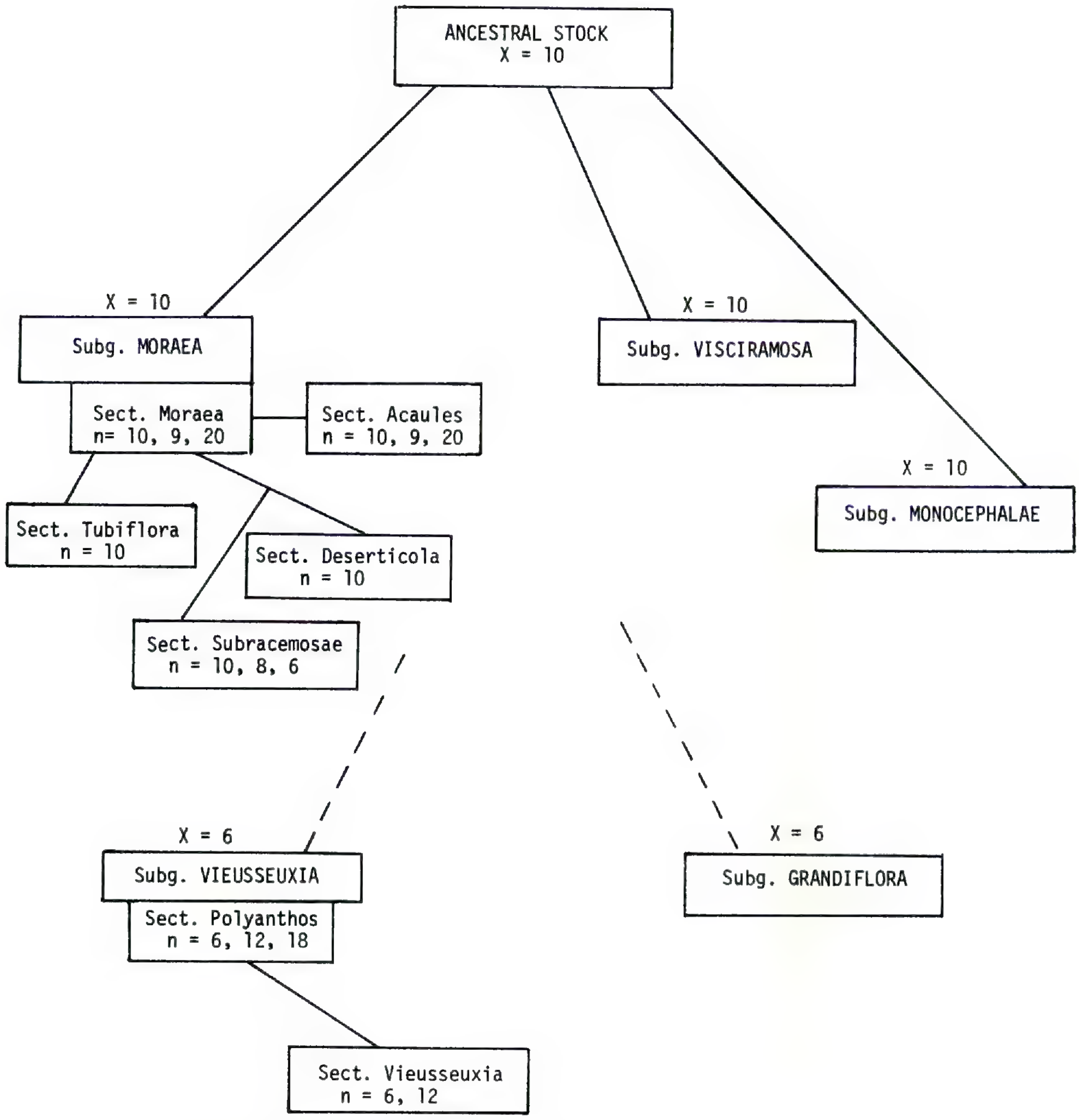

FIGURE 3. Diagrammatic representation of presumed phylogenetic relationships of subgenera and sections in *Moraea*.

genera *Vieusseuxia* and *Grandiflora*, as well as *M. fugax* and *M. filicaulis* of subg. *Moraea*, each with $x = 6$, are probably not of particularly recent origin and their independent derivation (Fig. 3) suggests that this low chromosome number has considerable selective value. Once this was achieved, rapid evolution followed. The two subgenera with $x = 6$, subg. *Grandiflora* and subg. *Vieusseuxia*, comprise by far the largest number of species with ± 75% of the species. Though both subgenera may be of some age, a very recent spurt of evolution appears to have occurred resulting in the numerous species now found, particularly in the Mediterranean region of South Africa.

The hypothesis that $x = 10$ is the ancestral condition in *Moraea* is consistent with the previously expressed view that the immediate ancestor of *Moraea* was the genus *Dietes* ($x = 10$). *Dietes*, a small genus of five African species with one

species on Lord Howe Island, Australia, is comprised of quite large, evergreen plants, usually with a branched inflorescence, a fan of many equitant leaves, and a simple *Iris*-like flower with subequal spreading tepals, petaloid styles, and distinct crests. Major primitive features are the evergreen habit, absence of a perianth tube (as in most *Moraeas*), free stamens (joined in *Moraea*), and a large persistent rhizome.

The flower of *Moraea* is similar, except in obviously highly derived forms, although the inner tepals are usually smaller than the outer and the stamens almost always are joined in a column. The vegetative form of *Moraea* is, in contrast, much modified; the plant is deciduous, the rootstock is a corm, and the leaves are much reduced. The usual iridacaeous feature, the equitant leaf, is so reduced in *Moraea* that it is represented by the morphological equivalent of an extended leaf sheath, which is terminated by a small equitant apex (Arber, 1921; Lewis, 1954; Goldblatt, 1971a). All these features suggest that *Moraea* evolved in response to strong seasonal conditions possibly when either increasing cold or more arid climates prevailed. The underground corm would thus insure survival during unfavorable periods, while the reduction in size and branching and the nature of the leaf suggest an adaptation for rapid growth during a short growing period.

Extreme cold such as accompanied by the severe glaciations in the Northern Hemisphere and a corresponding short growing season did not prevail in Africa either during the later Tertiary when *Moraea* was probably evolving or more recently. Seasonal aridity, however, does occur today and has been part of the African climatic regime since at least mid-Tertiary in areas where *Moraea* is found. As the climate deteriorated from the Miocene onward, areas bordering the tropics must have been subjected to increasing stress as a result of both summer drought and cooler winters. Such a setting is one in which *Moraea* is believed to have evolved.

That the majority of species of *Moraea* including all those with a basic chromosome number of $x = 10$ occur today in the southwestern Cape and Namaqualand under a winter rainfall, dry summer regime, might suggest this area as the place of origin of the genus. However, the origin of the genus under such a climate seems untenable in view of the current belief that true Mediterranean type climates such as found in the southwestern Cape may not be much more than three million years old (Raven, 1973; Axelrod, 1973). *Moraea* is almost certainly considerably older and the primitive species of *Moraea* that now all occur in the Cape region may perhaps be relicts surviving only in this area owing to lack of competition. Alternatively, *Moraea* may have evolved entirely in this area under different climatic conditions.

It is, however, evident that the extraordinary radiation of *Moraea* in the Cape winter rainfall area is a direct result of the violent climatic fluctuations during the Pleistocene (e.g., Schalke, 1973) and the development of an extreme Mediterranean climate. Most of the present day Cape species are therefore probably of quite recent origin, probably less than 1–2 million years old, with the more localized species which occupy specialized habitats probably only a few tens of thousands of years old.

The center of evolution of *Moraea* is perhaps somewhere to the north of the

Cape winter rainfall zone in the interior of central Southern Africa, between latitudes 10° and 30°S which includes Namaqualand where several primitive species occur today. Parts of this region are arid semidesert while others are dry savanna, and this area is perhaps the most sensitive to climatic changes such as envisioned in the evolution of *Moraea*. Today, with the exception of the eastern mountain ranges and Namaqualand, this area is the habitat for few species of *Moraea* but contains a scattering of unrelated species. It is of interest, though, that the most primitive species of *Ferraria*[8] (base number $x = 10$), *F. glutinosa*, the only freely branched species of this otherwise Cape genus, occurs throughout this zone. It is allied to *Moraea* and perhaps evolved from *Dietes* in much the same way as *Moraea*. It seems likely that the ancestors of the modern species of *Moraea* may also once have inhabited this region.

The occurrence of the specialized subgenera *Grandiflora* and *Vieusseuxia* in the eastern mountains of Africa as far north as Ethiopia, with subg. *Grandiflora* also in West Africa, is probably a fairly recent development. These subgenera are undoubtedly the most specialized and thus probably of comparatively recent origin, although the montane habitat may be of considerable age.

Nomenclatural Notes and New Species

Although a detailed revision of the winter rainfall area species of *Moraea* is planned, and this is where most nomenclatural changes will be made, I have used what are now known to be correct specific names in this paper and several changes in current usage require explanation. The cytology of 4 undescribed species was discussed earlier in this paper and these new species are described below.

1. **Moraea gawleri** Spreng., Syst. Veg. 5 (Index): 462. 1828, nom. nov. pro *M. crispa* (L.f.) Ker.

M. crispa (L.f.) Ker, Curtis's Bot. Mag. *tab.* 754. 1804, hom. illeg., non Thunb., 1787.
Iris crispa L.f., Suppl. Pl. 98. 1781.
Moraea undulata Ker, Gen. Irid. 43. 1827, hom. illeg., non Thunb., 1787.
M. decussata Klatt, Abh. Naturf. Ges. Halle 15: 367. 1882; Erganz. 33. 1882, syn. nov.

Moraea gawleri, a new name proposed by Sprengel (1828) for the illegitimate homonym *M. crispa* (L.f.) Ker, is the correct name for the species variously known in herbaria as *M. crispa* (L.f.) Ker, *M. undulata* Ker, or *M. decussata* Klatt. The former two names are later homonyms while *M. gawleri* predates Klatt's *M. decussata* by more than 50 years.

2. **Moraea serpentina** Baker, Handbook Irid. 52. 1892.

Moraea framesii L. Bol., S. African Gard. 17: 418. 1927, syn. nov.

Moraea serpentina Baker is regarded as a conspecific with *M. framesii*, a common N.W. Cape and Namaqualand species. The type specimens of these two species are very alike and fit within the author's concept of *M. serpentina*.

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[8] The chromosome count for this species, made by the writer, is as yet unpublished.

3. **Moraea lugubris** (Salisb.) Goldbl., comb. nov.

Ferraria lugubris Salisb., Prod. Stirp. 42. 1796. TYPE: Cape Town, base of Devils Peak, *Thunberg* (UPS, lectotype).
Moraea iriopetala L.f., Suppl. Pl. 98. 1781, nom. illeg., superfl. pro *M. vegeta* L.
M. plumaria (Thunb.) Ker, Konig & Sims Ann. Bot. 1: 240. 1805, syn. nov.
Iris plumaria Thunb., Diss. Irid. no. 16. 1782, nom. illeg., superfl. pro *M. vegeta* L.
Moraea mira Klatt, Trans. S. African Philos. Soc. 3: 202. 1885, syn. nov.

Moraea lugubris (Salisb.) Goldbl., better known as *M. plumaria* (Thunb.) Ker has had a complex nomenclatural history. This plant was first given the name *M. iriopetala* by the younger Linnaeus, this being known from the inscription on several specimens in the Linnaean herbarium. However, the way in which *M. iriopetala* was described makes the name illegitimate, and in fact nomenclaturally a superfluous synonym for *M. vegeta* L. The younger Linnaeus actually described two varieties under *M. iriopetala*, one (presumably the typical variety) listed with the synonym *M. vegeta* L., and a second with the name *M. juncea* L. cited. Subsequently, Thunberg (1782) described *Iris plumaria*, a species clearly matching the specimens annotated *M. iriopetala* in the Linnaean Herbarium. Unfortunately Thunberg cited as synonyms not only the illegitimate name *M. iriopetala*, but also *M. vegeta* and *M. juncea*, thus invalidating *Iris plumaria*. Before Ker (1804) transferred *Iris plumaria* to *Moraea* in which genus it can be treated as a legitimate new species, Salisbury (1796) provided a new name for it, *Ferraria lugubris*. Salisbury cited *M. iriopetala* and *Iris plumaria* as synonyms but both names, being illegitimate, were correctly not used. Salisbury's *Ferraria lugubris* is clearly a synonym of Thunberg's *Iris plumaria* and the younger Linnaeus's *M. iriopetala* (as this applies to material in the Linnaean collection), and Salisbury may even have seen the Linnaean specimens so annotated. Thunberg's specimens of this species in the Thunberg Herbarium at Uppsala are chosen as lectotype.

4. **Moraea fergusoniae** L. Bol., S. African Gard. 19: 294. 1929.

Moraea fimbriata Klatt, Linnaea 34: 561. 1866, hom. illeg., non Loisel, 1822; syn. nov.

Moraea fergusoniae and *M. fimbriata* are names both in current use. Although when described, *M. fergusoniae* was believed distinct from *M. fimbriata*, this is not the case. The later name *M. fergusoniae* must however be used as *M. fimbriata* is a later homonym.

5. **Moraea vegeta** L. is the correct name of the species known for many years as *M. juncea* or as *M. tristis*. For an explanation of this change in usage see Barnard & Goldblatt (1975).

6. **Moraea filicaulis** Baker, Handbook Irid. 56. 1892.

Moraea diphylla Baker, Bull. Misc. Inform. 1906:24. 1906, syn. nov.

Moraea filicaulis is an older name for *M. diphylla* and the latter is reduced to snyonymy.

7. **Moraea elsiae** Goldbl., nom. nov. pro *Homeria simulans* Baker.

Homeria simulans Baker, Fl. Cap. 6: 529. 1896. TYPE: South Africa, Cape, Kenilworth, Cape Peninsula, *H. Bolus 7931* (BOL, holotype; K, MO, isotypes).

Moraea elsiae is a new name proposed here for *Homeria simulans* Baker. In spite of the floral similarity of *M. elsiae* to *Homeria*, the whole appearance of the plant with its many branches, sticky internodes, short obtuse bracts, and oily corm tunics makes it clear that the plant is correctly placed in *Moraea* subg. *Viscira-mosa*. The original reason for placing it in *Homeria* was the reduced style crests but this character is now recognized as occurring in several species of *Moraea* also (Goldblatt, 1971b). The species is named in honor of Miss Elsie Esterhuysen, the indefatigable Cape botanist who is endeavoring to conserve its best known locality, Kenilworth Racecourse in Cape Town. A new name was necessary as *M. simulans* Baker (= *Gyrandriris*) blocks the transfer from *Homeria*.

8. For the explanation of the usage of *Moraea stricta* Baker (for *M. trita* N.E. Br.), *M. falcifolia* Klatt (for *M. fasciculata* and *M. galaxioides*) and *M. elliotii* (for *M. macra* and *M. stewartae*) see Goldblatt (1973).

NEW SPECIES

Subg. *Moraea* sect. *Moraea*

1. **Moraea margaretae** Goldbl., sp. nov. TYPE: South Africa, Cape, Namaqualand, pipeline track, SW of Nababeep, *Goldblatt 628* (BOL, holotype; K, MO, PRE, S, isotypes).

Planta parva, ad 15 cm alta, ramosa. Folia producta 2–3, lineares, glabra, canaliculata an teres supra. Flores pallidi-lutei; tepala exteriora ad 3 cm longa, limbis 2 mm longis; tepala interiora erecta, lanceolata.

Plants to 15 cm high, usually 1–2 branched. Corm 5–7 mm in diameter, the tunics brown, coarsely fibrous, the inner layers entire. Leaves 2–3, linear, canaliculate, often terete and twisted near apex. Stem glabrous, branching usually from the base. Spathes herbaceous, with dark brown, acute or lacerated apices; inner spathe 3–4.5 cm long, outer 2–3 cm long. Flowers few, pale yellow; outer tepals 2–3 cm long with limb 1.5–2 cm, spreading to reflexed; inner tepals erect, spreading later, lanceolate, obtuse, to 2.0 cm. Filaments ± 5 mm long, joined for 4 mm; anthers 4–5 mm, red. Style branches ± 7 mm with lanceolate crests 6–10 mm long. Capsule and seeds unknown. Chromosome number $2n = 40$.

Flowering time: Late September and October.

Distribution: Coarse sandy soils in Namaqualand; more common than the record suggests.

This diminutive species is known from few collections but is nevertheless quite common in central Namaqualand, a very arid region of the Cape winter rainfall region. Its pale yellow, strongly veined flowers conform to the usual pattern for the genus, but its vegetative features, especially the characteristic branching from near the base and its 2 or 3 produced leaves, indicate a position in section *Moraea* and suggest particularly a close relationship with *M. papilionacea*. The basic chromosome number of $x = 10$ confirms its sectional position. The diploid number of $2n = 40$ for the type population (only two individuals examined) suggests this species is tetraploid. *Moraea margaretae* is named after my wife whose company and help on field trips has been invaluable.

SOUTH AFRICA. CAPE: 29.17 (Springbok):[9] 4 km W of Steinkopf (BA), *Goldblatt 2775* (MO). Koufontein, Steinkopf dist. (BC), *Herre s.n.* (STE 11835). Pipeline road S of Nababeep (CA), *Goldblatt 628* (BOL, K, MO, PRE, S). 8 km E of Nababeep (CB), *Goldblatt 3061* (NBG, MO, PRE).

30.17 (Hondeklipbaai): 8 km N of Garies (BD), *Leighton 1129* (BOL). Brackdam, hills, *Schlechter 11120* (BM).

Without precise locality: Namaqualand minor, *Scully 134* (BM).

Subg. *Vieusseuxia* sect. *Vieusseuxia*

2. **Moraea thomasiae** Goldbl., sp. nov. TYPE: South Africa, Cape, Koo dist., Burgher's Pass, *Goldblatt 2422* (MO, holotype; K, NBG, PRE, S, isotypes).

Planta parva, 15–20 cm alta, simplex. Cormus ad 1 cm diameter, tunicis atrobrunneis ad nigris. Folium productum solitarium, cananiculatum, glabrum, inflorescentiam excedentum. Flores lutei; tepala exteriora ad 3.5 cm longa, limbis ad 2 cm longis; tepala interiora lanceolata, ad 2 cm longa.

Plants small, slender, 15–20 cm high. Corm about 1 cm in diameter, the tunics dark brown to black. Produced leaf solitary, ± basal, linear, about 3 mm wide, glabrous, exceeding the inflorescence. Scape simple. Spathes herbaceous with brown attenuate apices; inner spathe to 6 cm long, outer about half the length of the inner. Flowers yellow; outer perianth segments with a narrow, long, erect claw, 1.5 cm long, the limb reflexed, about 2 cm long; inner segments erect, narrowly lanceolate, up to 2 cm long. Filaments about 5 mm long, free almost to the base; anthers about 6 mm long. Style branches about 1.5 cm long, bearing linear crests about 1 cm long. Capsules and seeds not known. Chromosome number $2n = 12$.

Flowering time: July to mid September.

Distribution: Clay and shale slopes, usually on a south facing slope, in the Montagu and Worcester districts.

Moraea thomasiae grows in the Worcester and Montagu districts of the south western Cape in fairly arid, semikaroid areas, where it grows characteristically on south facing shale slopes. It is a very distinct species with no close relatives. Its single leaf and slender, often unbranched stem suggests that it is best placed in sect. *Vieusseuxia*. Its simple flowers with entire inner tepals are not usual in the section, although these are known, for example, in *M. incurva*. The karyotype with $2n = 12$, supports its subgeneric placement, but the predominantly acrocentric chromosomes do not suggest a close relationship with other species in sect. *Vieusseuxia*. Its somewhat superficial similarity to the *M. angusta* complex is belied by its entirely canaliculate leaf, brown to black corm tunics, and above all, its very acute bract leaves and spathes. The difference in karyotype (*M. angusta* has $2n = 20$) makes it quite clear that *M. thomasiae* is not even remotely related to *M. angusta*. The species is named in honor of Margaret Thomas, an enthu-

[9] Note on Citation of Specimens.—The arrangement of specimens examined, following the taxonomic treatment and discussion of each species, is based on the system currently gaining acceptance in South Africa (Edwards & Leistner, 1971). The system is based on a grid, and geographical degrees of latitude and longitude define each grid which is numbered accordingly. The one degree square grids are also designated by the name of a major town within it. Grids are divided into four quarters labelled from left to right A, B, C, or D and these quarter degree squares are again divided into four and labelled A, B, C, or D. Thus, all specimens are cited with data localizing them to one-sixteenth of a degree square.

siastic and untiring South African bulb grower and collector. The living material of the many species of Iridaceae she has provided me with is gratefully acknowledged.

South Africa. cape: 33.19 (Worcester): Hex R. Pass, near summit (BD), *Mauve & Oliver* (STE). Karoo Garden, Worcester (CD), *Bayer 7* (NBG); *Goldblatt 2422* (MO, NBG, PRE, K). Onse Rug Farm, Worcester dist., *Barker 9446* (NBG).

33.20 (Montagu): Oudeberg, Montagu dist. (CA), *Acocks 20539* (NBG, PRE). Burger's Pass, Koo dist. (DB), *Thomas s.n.* (BOL); *Mauve & Oliver 197* (STE). Vrolikheid, McGregor dist. (DD), *Jooste 154, 181* (both STE).

3. **Moraea debilis** Goldbl., sp. nov. type: South Africa, Cape, clay slopes SW of Caledon, *Goldblatt 673* (BOL, holotype; K, MO, PRE, S, isotypes).

Planta gracilis, ad 15–40 cm longa, ramosa. Cormus ad 1 cm diam., tunicis pallidis. Folium productum solitarium basale, canaliculatum, pubescentum an marginibus ciliatibus. Flores purpurei decolorentes ad malvini pallidi; tepala exteriora ad 2 cm longa; tepala interiora ad 1 cm longa, erecta, filiformia, plerumque tricuspidata.

Plants slender, 15–40 cm high, usually branched. Corm ± 1 cm in diameter, the tunics pale, finely fibrous. Leaf solitary, basal, linear, pubescent on outer surface and/or ciliate on margins, exceeding the inflorescence. Stem laxly branched, rarely simple, the bract leaves dry. Spathes herbaceous, or dry above, the apex attenuate or lacerated; inner spathe 4–5.5 cm long, outer ± half the inner. Flowers purple, fading to a pale mauve and becoming lightly speckled; outer tepals spreading, ± 2 cm long with a slender bearded claw and a lanceolate limb ± 1 cm long; inner tepals ± 1 cm long, erect, filiform, usually tricuspidate with the central cusp much exceeding the laterals. Filaments ± 5 mm long, joined for about half the length; anthers ± 5 mm long. Style branches ± 8 mm long, the crests lanceolate, to 3 mm. Capsule narrowly ovoid-clavate. Seeds angled. Chromosome number $2n = 12$.

Flowering time: Late September and October.

Distribution: Clay soils in the Caledon district, southwestern Cape.

This slender, almost spindly plant with its small mauve flowers and reduced inner tepals is clearly allied to the well known and widespread *Moraea tripetala*. *M. debilis* is known from several collections, all from the Caledon district of the south western Cape, where it grows in clay soils amongst small shrubs and is typically late flowering. It is distinguished by its fine, pale corm tunics, pubescent leaf and small flowers with their threadlike, trifid to tricuspidate inner tepals. The karyotype, with a diploid number of $2n = 12$, is very characteristic of *M. tripetala* and its close allies.

South Africa. Cape: 34.19 (Caledon): SW of Caledon (AC), *Barnard s.n.* (BOL 30694); *Goldblatt 673* (BOL, K, MO, PRE, S). Between Bot River and Caledon, *Mauve 4893* (PRE). Ca. 12 km E of Caledon (BA), *Barker 10851* (NBG).

Without precise locality: Caledon dist., *Pappe s.n.* (SAM 70709); *Leipoldt 3562* (BOL); *Schlechter 5527* (BOL, PRE).

4. **Moraea caeca** Barnard ex Goldbl., sp. nov. type: South Africa, Cape, top of Dasklip Pass near Porterville, *Goldblatt 678* (BOL, holotype; K, MO, PRE, S, isotypes).

Planta 20–40 cm alta, raro ramosa. Folium productum, solitarium, canaliculatum, inflorescentiam excedentum. Flores malvescenti; tepala exteriora ad 3 cm long, ungue canalicu-

lato, pubescenti, limbis obovatis, ca. 2 cm latis; tepala interiora tricuspidata, cuspide centrale, 5–8 mm longa, lineare, cuspidibus lateribus 2 mm longis, obtusis.

Plants slender, 20–40 cm high. Corm ± 1 cm in diameter, with light brown fibrous tunics. Leaf solitary, linear, glabrous, exceeding the inflorescence. Stem glabrous (occasionally pubescent), usually simple. Spathes herbaceous or dry above with brown attenuate apices; inner spathe ± 5 cm long, outer to ± 2.5 cm. Flowers mauve-lilac with a small yellow or black nectar guide; outer tepals spreading, ± 2.8 cm long with an erect, channelled, pubescent claw 8–12 mm long and a broadly ovate, spreading limb, to 1.8–2.2 cm wide; inner tepals tricuspidate, channelled, the central cusp 5–8 mm long, laterals to 2 mm. Filaments 2–3 mm long, united near the base only; anthers dark, ± 5 mm long. Style branches ± 5 mm long, the crests acute to obtuse, to 7 mm long. Capsule clavate, to 1.5 cm. Seeds angular. Chromosome number $2n = 12$.

Flowering time: Late September and October.

Distribution: The Piketberg and Twenty Four Rivers Mountains above Porterville, and locally on the Cape Peninsula, southwestern Cape; confined to sandy soils.

Moraea caeca is an attractive late-flowering species allied to the "peacock Moraeas," the usually large flowered, highly colored species with very broad, outspread outer tepals with conspicuous nectar guides. This species is smaller than others of the group and instead of the bright nectar guide of yellow circled with contrasting colors, the guide is small and dark or absent. It grows in sandstone areas and is known from three somewhat isolated areas, the Piketberg and the Twenty Four Rivers Mountains on opposite sides of the Piketberg–Porterville valley and from a single collection from the Karbonkelberg on the Cape Peninsula. The karyotype with $2n = 12$ is similar to that of *M. neopavonia* and *M. villosa* (although the latter is tetraploid) in the number of metacentric and submetacentric chromosomes and in the position of the satellite.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Kloof on SW side of the Piketberg (DC), *Barnard s.n.* (BOL). Moutons Valei, *Marloth 11509* (PRE). Hills NW of Moutons Valei, *Pillans 7488* (BOL). Piketberg (DD), *Vlok s.n.* (NBG 58948). Beyond Piketberg on Redelinghuys road, *Barnard s.n.* (SAM 52394, BOL).

32.19 (Wuppertal): Dasklip (Cardouw) Pass above Porterville (CC), *Barker 7599* (NBG, STE); *Esterhuysen 16211* (BOL); *Goldblatt 678* (BOL, MO, K, PRE). Mountain above Porterville, *Loubser 856* (NBG).

33.19 (Worcester): Driebosch, Groot Winterhoek (AA), *Haynes 858* (STE).

34.18 (Simonstown): Karbonkelberg, Cape Peninsula (AB), *Salter 3288* (BM).

LITERATURE CITED

ARBER, A. 1921. The leaf structure of the Iridaceae considered in relation to the phyllode theory. Ann. Bot. (London) 35: 301–336.

AXELROD, D. I. 1973. History of the Mediterranean ecosystem in California. Pp. 225–277, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems: Origin and Structure. Springer-Verlag, New York.

BAKER, J. G. 1896. Irideae. *In* W. T. Thiselton-Dyer (editor), Flora Capensis. Vol. 6: 7–71. L. Reeve & Co., London.

BARNARD, T. T. & P. GOLDBLATT. 1975. A reappraisal of the application of specific epithets of the type species of *Moraea* and *Dietes* (Iridaceae). Taxon 24: 125–131.

DYER, A. F. 1963. The use of lacto-propionic orcein in rapid squash methods. Stain Technol. 38: 85–90.

EDWARDS, D. & O. A. LEISTNER. 1971. A degree reference system for citing biological records in Southern Africa. Mitt. Bot. Staatssamml. München 10: 501–509.

FERNANDES, A. & J. B. NEVES. 1961. Sur la caryologie de quelques Monocotyledones Africains. Compt. Rend. IVe Réunion A.E.T.F.A.T.: 458–463.

GOLDBLATT, P. 1971a. Cytological and morphological studies in the southern African Iridaceae. J. S. African Bot. 37: 317–460.

———. 1971b. *Moraea insolens*. Fl. Pl. Africa 41: *tab. 1639*.

———. 1973. Contributions to the knowledge of *Moraea* (Iridaceae) in the summer rainfall region of South Africa. Ann. Missouri Bot. Gard. 60: 204–259.

LEWIS, G. J. 1949. *Moraea angusta* (Thunb.) Ker and allied species. J. S. African Bot. 15: 115–120.

———. 1954. Some aspects of the morphology, phylogeny and taxonomy of the South African Iridaceae. Ann. S. African Mus. 40: 15–113.

LEWIS, W. H. 1966. Chromosomes of two *Moraea* (Iridaceae) from Southern Africa. Sida 1: 381–382.

RAVEN, P. H. 1973. The evolution of Mediterranean floras. Pp. 213–224, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems: Origin and Structure. Springer-Verlag, New York.

RILEY, H. P. 1962. Chromosome studies in some South African Monocotyledons. Canad. J. Genet. Cytol. 4: 50–55.

SAKAI, B. 1952. Zytologische Untersuchung bei Iridaceen Über die Karyotypen verschiedener Arte der Unterfamilie Iridoideae. Cytologia 17: 104–111.

SCHALKE, H. J. W. G. 1973. The Upper Quaternary of the Cape Flats Area (Cape Province, South Africa). Scripta Geol. 15.

EVOLUTION OF THE SANTA LUCIA FIR (*ABIES BRACTEATA*) ECOSYSTEM[1]

DANIEL I. AXELROD[2]

ABSTRACT

Abies scherrii Axelrod is described from the Miocene of western Nevada, and it resembles the living *A. bracteata* of the Santa Lucia Mountains, coast-central California, a unique endemic representing the sole member of the subgenus *Pseudotorreya*. Although the fossil species *A. chaneyi* Mason and *A. longirostris* Knowlton have previously been considered allied to *A. bracteata*, those species are extinct, they are not closely allied to *bracteata*, and they are only distantly related to living Asian firs. *A. scherrii* occupied an ecotone between broadleaved evergreen sclerophyll forest and mixed conifer forest during the Miocene in western Nevada, and its descendant *A. bracteata* has a similar occurrence today. The Miocene communities were much richer than the living, including species whose nearest descendants occur only in regions with summer rainfall, or now occupy more restricted areas in California. The latter include *Sequoiadendron* of the central and southern Sierra Nevada, species of *Chamaecyparis* and *Picea* that are confined to the Klamath-Siskiyou region of northwestern California, and species of *Abies* and *Pinus* that are largely subalpine in the Sierra Nevada. *Abies scherrii* and its associates shifted coastward as colder and drier climate developed over the interior. *Abies bracteata* has survived in a near-coastal climate where evaporation rate is not so high as in the interior or in areas to the south, and where it is largely removed from regular heavy winter snow and ice. Some of its associates were segregated into their present areas as the summer-dry mediterranean climate emerged in the Quaternary. *Sequoiadendron* was confined to the relatively drier and sunnier central and southern Sierra Nevada where there was sufficient light in an open forest to enable it to reproduce. *Chamaecyparis* and *Picea* were restricted to the northwest sector where there is a longer precipitation season, some summer rain, and where evaporation rate is lower than in the Sierra. Present subalpine species of *Abies*, *Pinus* and *Tsuga* were eliminated from the mixed conifer forest in the Sierra Nevada as evaporation rate increased during summer and produced conditions inimical for seedling establishment, though they still persist in the upper mixed conifer forest in moister, more equable areas to the northwest. *A. bracteata* may have had a wider distribution in the Coast Ranges during the moister phases of the Quaternary, together with the mixed conifer forest species. It was apparently restricted with them as drier, hotter climates spread during the later postglacial periods.

Santa Lucia fir (*Abies bracteata*) is confined to the middle and upper slopes of the Santa Lucia Mountains, coast-central California (Figs. 1–2). Among the 60-odd species and varieties of fir it is the sole member of the subgenus *Pseudotorreya*, the remainder representing the subgenus *Abies* (Liu, 1971). Its uniqueness is seen in the long-fusiform to ovoid-conical resinless winter buds, the cones with exserted awllike bracts 2 to 4 cm long, the sharply-pointed deep green needles like those of *Torreya*, the very thin bark (and hence the need for fire protection), and its tall spirelike habit that recalls that of *Abies lasiocarpa* or *Picea engelmannii* near timberline.

The problem of its geologic history was raised by the recent discovery of a slab of shale on which are preserved three cone scales with long, exserted awllike bracts of a fir that indubitably represent a species similar to the living *A. bracteata*. This fossil, from the Late Miocene (13 m.y.) Purple Mountain flora of western Neveada, supplements a needle collected earlier at a nearby site that is similar to

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ANN. MISSOURI BOT. GARD. 63: 24–41. 1976.

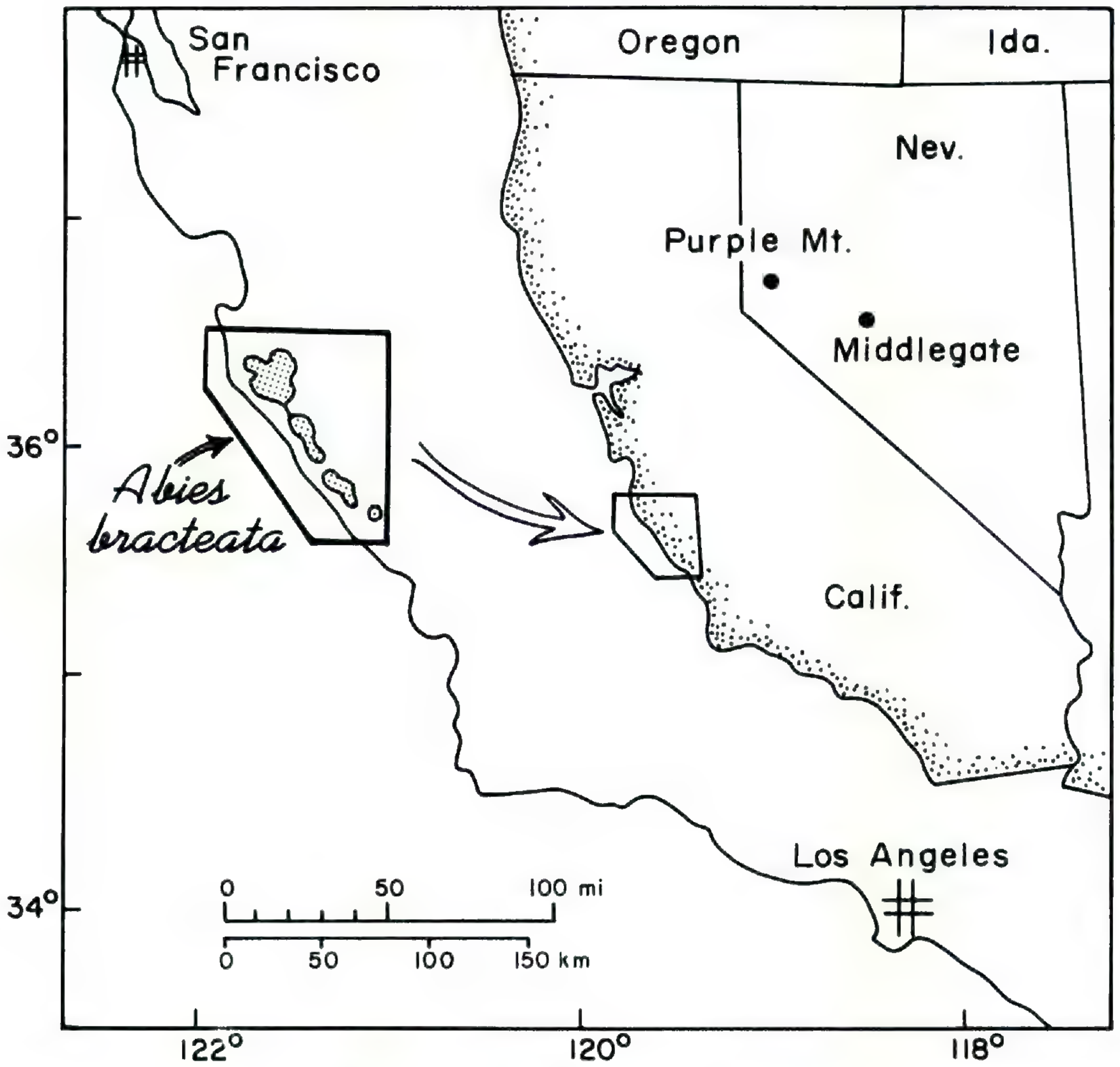


FIGURE 1. Present occurrence of *Abies bracteata* (see Griffin & Critchfield, 1972), and of the closely similar *A. scherrii* in the Miocene of Nevada.

those produced by *A. bracteata.* In addition, new collections of the slightly older Middlegate flora (Axelrod, 1956), situated about 80 miles southeast, have yielded a needle and winged seed that also represent fossil Santa Lucia fir.

In each area the associated flora is composed of broadleaved sclerophylls (*Arbutus*, *Castanopsis*, *Lithocarpus*, *Quercus*) similar to species that live with Santa Lucia fir today. Both floras also have species of *Abies*, *Picea*, *Pinus*, *Pseudotsuga*, *Chamaecyparis*, *Sequoiadendron* (Figs. 4–20) and numerous dicots that now contribute to mixed conifer forest in the Sierra Nevada, Siskiyou-Klamath Mountains, and the high Coast Ranges. The Purple Mountain and Middlegate records thus provide a basis for comparing the Miocene ecosystem at two different sites of slightly different age, and for outlining the post-Miocene history of the community.

GEOLOGIC OCCURRENCE

PURPLE MOUNTAIN FLORA

The site that yielded the Purple Mountain fossils allied to the living Santa Lucia fir is in the Truckee River canyon southwest of Wadsworth, Nevada (Figs. 1, 3). Regional geologic reports (Rose, 1969; Bonham, 1969), coupled with my

FIGURE 2. Santa Lucia fir on east slope of Cone Peak, altitude ~ 4,300 feet. *Pinus lambertiana* on left. *Quercus chrysolepis* in foreground is part of the evergreen sclerophyll forest that covers the nearby and distant slopes and includes *Arbutus menziesii*, *Lithocarpus densiflorus*, and *Quercus wislizenii* as codominants, all represented by fossils associated with *Abies scherrii* in the Nevada Miocene.

own more detailed mapping in this local area, show that the plant-bearing beds are in the lower part of the Chloropagus Formation. It is composed chiefly of andesite flows but includes mudflow breccias and interbedded thin sections of limestone and organic shale that contain the remains of plants that lived on the borders of shallow ponds and small lakes. The Chloropagus is overlain by welded dacitic tuffs of the Kate Peak Formation, dated in the nearby region at 12–13 m.y. (Bonham, 1969). The Chloropagus rests unconformably on a 50-foot rhyolite tuff that has been correlated with the Old Gregory Formation in the hills west of Fallon. It lies unconformably on black flows of Alta Andesite, which in turn rests on the varicolored welded tuffs of the Hartford Hill Rhyolite (22 m.y.). The Hartford Hill covers a peneplaned basement of high grade metamorphic rocks intruded by granodiorite of Cretaceous age.

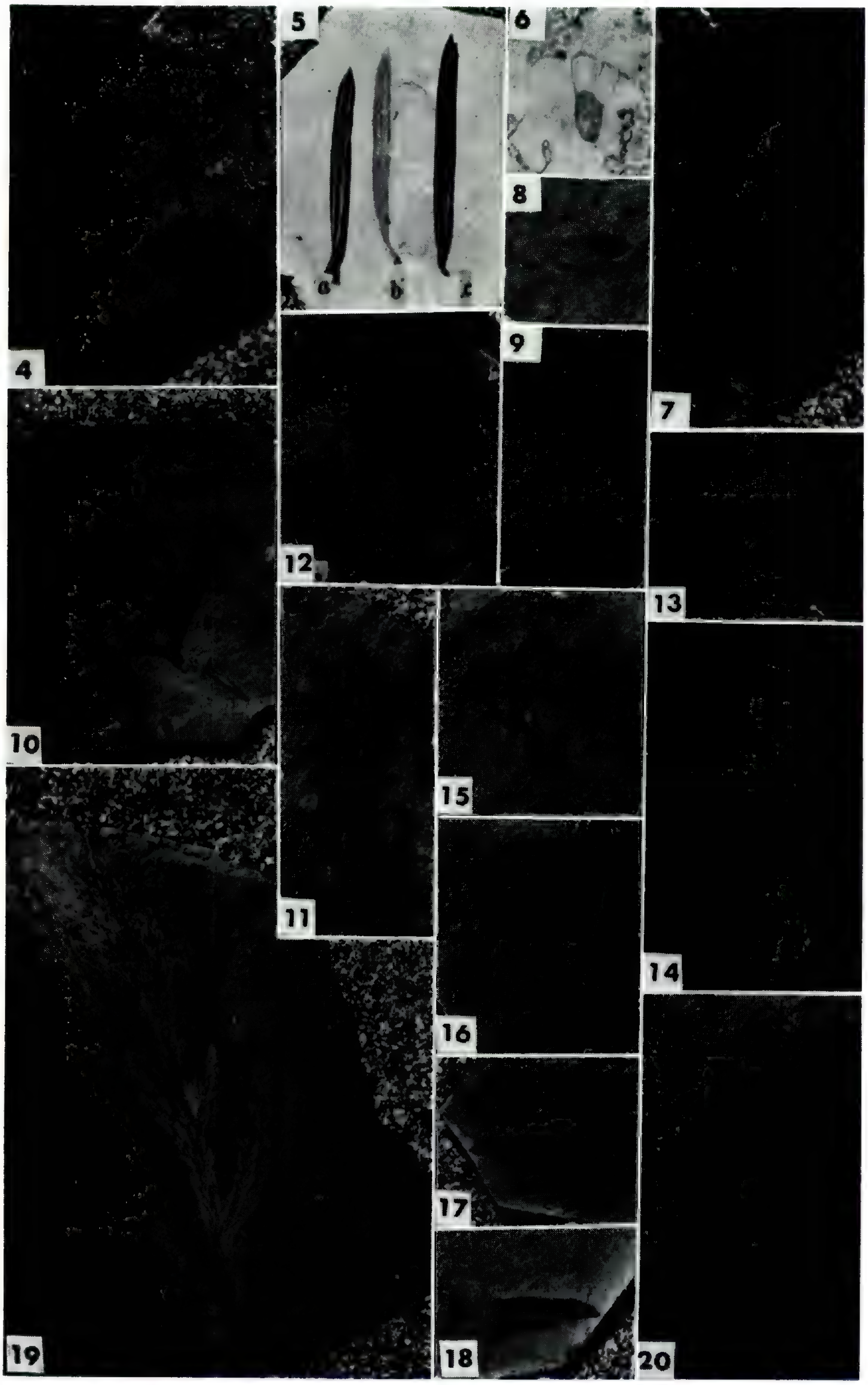
FIGURE 3. The Late Miocene Purple Mountain flora occurs in thin lake beds intercalated with andesites of the Chloropagus Formation on the low spur at the right, in the bank of the drainageway, and at the position of the observer. View is north, across Truckee River floodplain.

Flows in the basal part of the Chloropagus Formation in Fort Defiance Canyon 10 miles north of the fossil locality have been dated as 14 m.y., and a vitric tuff in the upper part of the sequence in Pierson Canyon 5 miles northwest is 13 m.y. The flora is therefore about 13.5 m.y. and is correlative approximately with the Late Miocene Fallon, Chloropagus, and Aldrich Station floras in the nearby region (Axelrod, 1956).

MIDDLEGATE FLORA

This flora comes from a site on the north side of Middlegate basin, 5 miles northwest of Eastgate, Nevada (Axelrod, 1956). The plants are preserved in white to light gray, well-bedded opaline shales interbedded with fine vitric tuff now altered to bentonite. The shales are 50–80 feet below the top of the Middlegate Formation. They grade down into soft dark mudstone, very thin opaline shale, and with local conglomerates situated opposite the mouths of small streams that entered the lake. The Middlegate Formation rests on diverse welded tuffs and flows of the Clan Alpine Volcanics directly north of the site. Since the flora was derived from volcanic slopes facing south, the warm dry exposure accounts for the rich representation of sclerophylls there.

The Middlegate is overlain conformably by fine sandstone, mudstone, tuff, and conglomerate of the Monarch Mill Formation, the basal part of which has now yielded a rich (30+ taxa) mammal fauna of transitional Hemingfordian–Barstovian (~ 16 m.y.) age.



FIGURES 4–20. Purple Mountain conifers associated with *Abies scherrii*.—4. *Abies scherrii* Axelrod, no. 5489.—5b. *Abies scherrii* Axelrod, no. 5491 from Middlegate; 5a, 5c. *Abies bracteata* needles for comparison.—6. *Abies scherrii* Axelrod, no. 5492 from Middlegate.—7–9. *Pseudotsuga sonomensis* Dorf, nos. 5493–5495.—10–11. *Chamaecyparis sierrae* Condit, nos. 5496–5497.—12. *Abies concoloroides* Brown, no. 5498.—13–14. *Pinus quinifolia* Smith, nos. 5501–5502.—15–16. *Abies klamathensis* Axelrod, nos. 5499, 5500.—17–18. *Picea sonomensis* Axelrod, nos. 5503, 5504.—19–20. *Sequoiadendron chaneyi* Axelrod, nos. 5505, 5506.

Systematic Considerations

The Nevada occurrences of a Miocene fir similar to the living *A. bracteata* is not the first report of a fossil that has been presumed related to it. *Abies chaneyi* Mason from Oregon (Mason, 1927; Chaney & Axelrod, 1959) and *A. longirostris* Knowlton from Colorado (Knowlton, 1923; MacGinitie, 1953) have also been considered allied to *A. bracteata*. However, comparisons now indicate they are not closely related to it, and some of these fossils certainly represent genera other than *Abies*. Thus, it is necessary first to clarify the status of the fossil records that have been presumed allied to *A. bracteata*, following which the history of Santa Lucia fir, and the community of which it forms a part, can be outlined in provisional manner.

Abies scherrii Axelrod sp. nov.—Figs. 4, 5b, 6.

Cone scales 9–12 mm broad, 6–8 mm long, broadly oblong to ovate, distal end truncate to broadly rounded, proximal part truncated, with thin, straight woody peg of attachment; bract exserted, over 2.3 cm long, awllike, 1 mm wide for most of length but widening to 2 mm in proximal 3 to 4 mm; lateral appendages not visible on exposed upper surface. Needles 2.0–2.8 cm long, broadest at middle, 2.5 mm; apex sharply acuminate, petiole somewhat curved, sharply truncated. Winged seed 12 mm long, wing terminal, 5 mm long, somewhat torn, about 5 mm wide distally; seed long-oval, 7 mm long, 3 mm broad.

This species is represented in the Purple Mountain flora by a slab containing 3 cone scales with bracts and by a second specimen on which is a poorly preserved needle. In the Middlegate flora a winged seed and a needle are referred to this species.

The cone scales and attached bracts are similar to those of the living *A. bracteata* of the Santa Lucia Mountains, coast-central California. The lateral lobes of the bract are not visible, but this appears to be the result of curling so that they cannot be seen on the lower (inner) preserved surface. The needles and the single winged seed are also similar to those produced by the living Santa Lucia fir.

This species is named for Annette K. Scherr, a student in my course in Forest History who, during a class field-trip to the Purple Mountain area, collected the slab of shale on which are preserved the diagnostic cone scales of fossil Santa Lucia fir, *Abies scherrii*.

Occurrence: Nevada, Purple Mt.: U.C. Mus. Pal. holotype no. 5489, hypotype no. 5490. Nevada, Middlegate: U.C. Mus. Pal. hypotype nos. 5491, 5492.

Abies chaneyi Mason, Publ. Carnegie Inst. Wash. 347: 149, *pl. 4, figs. 1* and *7* (winged seeds only), *fig. 2*. 1927. Chaney & Axelrod, Publ. Carnegie Inst. Wash. 617: 137, *pl. 11, fig. 3*. 1959. Axelrod, Univ. Calif. Publ. Geol. Sci. 51: 141 (winged seeds only). 1964.

These cited specimens are winged seeds except for one that represents a cone scale with attached bract (Mason, pl. 4, fig. 2 only). The seeds have a slender, generally oblong to long-oval outline and the long narrow wing is attached high

up on the seed and is not appreciably widened or asymmetrical distally. The cone scale has a long exserted bract that is much wider at the distal edge of the scale than those of the living *A. bracteata.*

These fossils are not closely related to any living fir. Although the winged seeds resemble those produced by the living *A. bracteata*, those of other species—notably *A. chensiensis* Van Tiegham of central and southern China and *A. delavayi* Franchetti of southern China—are also similar to them. The winged seeds of *A. chaneyi* resemble those of *A. longirostris* Knowlton from the Creede flora of Colorado (Knowlton, 1923), though the Creede specimens tend to average somewhat smaller in size. However, the Creede fir has cone scales with exserted bracts that are inseparable from the Mascall fossil (Mason, 1927: 4, fig. 2). In this regard, the Creede *A. longirostris* appears distantly related to *A. delavayi* of southern China, as judged from the winged seeds as well as the conspicuously exserted acuminate bract. Further affinity is also seen in the fact that typical fir foliage is well represented in the Creede flora. It is like that produced by many montane species, with the needles curved upward on the branchlets, a feature also exhibited by *A. delavayi.*

Present evidence indicates that *A. chaneyi* is more nearly related to *A. longirostris* Knowlton than to any other fossil or living fir, and it may have been derived from the Creede species. Although both species seem distantly related to *A. delavayi* of southern China, there is no evidence of any close affinity between them and the living *A. bracteata* of the Santa Lucia Mountains.

Occurrence: Oregon, Mascall: U.C. Mus. Pal., holotype no. 135, hypotype no. 5488, A, B (on same slabs as foliage specimens of *Cephalotaxus*, = "*Abies chaneyi*" branchlet, nos. 134, and 136), 2826, 2828 (its counterpart), homeotype no. 2827. Oregon, Beulah: U.C. Mus. Pal. homeotypes nos. 779–780 (winged seeds only).

Cephalotaxus bonseri (Knowlton) Chaney & Axelrod, Publ. Carnegie Inst. Wash. 617: 136, *pl. 11, fig. 13.* 1959 (see synonymy).

Abies chaneyi Mason, Publ. Carnegie Inst. Wash. 346: 149, *pl. 4, figs. 1, 6* (counterparts of twig; not winged seed which remains *A. chaneyi* Mason). Chaney & Axelrod, Publ. Carnegie Inst. Wash. 617: 137, *pl. 11, figs. 1–2* only (fig. 3 remains *A. chaneyi* Mason). 1959. Axelrod, Univ. Calif. Publ. Geol. Sci. 51: 141. 1964 (in part).

Torreya bonseri (Knowlton) LaMotte, Publ. Carnegie Inst. Wash. 455: 108, *pl. 3, fig.* 9. 1936.

The above-cited specimens of *Abies chaneyi* are similar to the leafy twigs and needles of *Cephalotaxus bonseri*, a species abundantly represented in the Mollala flora of western Oregon, and known also from the Spokane (Latah) and Neroly floras of Washington and California, respectively (Chaney & Axelrod, 1959: 136). The needles are not *Abies* because they do not have the typical rounded bases, nor are the petioles twisted prominently as in *A. bracteata.* Furthermore, the leafy twigs do not reveal the rounded leaf scars that are diagnostic of *Abies.* However, the longitudinal ridging on the fossil twigs is like that on the twigs of the living *Cephalotaxus fortunei* of central China, which bear long, sharply acuminate needles like the fossils, and they often are curved in a falcate manner much like the fossil foliage.

Occurrence: Mascall, Ore. hypotype nos. 134 and 136 (counter parts), homeotype no. 2829 (leafy branch); Stinking Water, Ore.: hypotypes nos. 2830, 2831, homeotypes nos. 2832,

2833; Beulah, Ore.: homeotypes nos. 8573–8579 (needles only); 49-Camp, Nev.: hypotype no. 777.

Summarizing, *Abies scherrii* from the Middle and Late Miocene of western Nevada is similar to the living *A. bracteata*. Reexamination of the fossil *A. chaneyi* Mason and *A. longirostris* Knowlton, previously considered related to *A. bracteata*, shows that they are not allied to it. They seem related to one another, and may be extinct members of an alliance of present Asian distribution, of which *A. delavayi* of southern China is a surviving relict.

Composition

As now known, *Abies scherrii* occurs in the Purple Mountain and Middlegate floras of western Nevada. Among its associates that are common to both floras are the species listed in Table 1. As might be expected, each flora has species that are not now known from the other site. Species in the Purple Mountain flora that are not recorded at Middlegate are listed in Table 2.

Table 1. Species associated with *Abies scherrii* in both the Purple Mountain and Middlegate floras.

Fossil Species	Similar Living Species	Fossil Species	Similar Living Species
Abies concoloroides	*A. concolor*	*Lithocarpus klamathensis*	*L. densiflorus*
Abies klamathensis	*A. shastensis*	*Quercus hannibalii*	*Q. chrysolepis*
Picea sonomensis	*P. breweriana*	*Mahonia simplex*	*M. japonica; M. lomariifolia*
Picea magna	*P. polita*		
Pinus quinifolia	*P. monticola*	*Mahonia reticulata*	*M. pinnata-insularis*
Pseudotsuga sonomensis	*P. menziesii*	*Amelanchier alvordensis*	*A. alnifolia*
Chamaecyparis sierrae	*C. lawsoniana*	*Cercocarpus antiquus*	*C. betuloides*
Sequoiadendron chaneyi	*S. giganteum*	*Cercocarpus holmesii*	*C. paucidentatus*
Populus eotremuloides	*P. trichocarpa*	*Heteromeles sonomensis*	*H. arbutifolia*
Populus payettensis	*P. angustifolia*	*Lyonothamnus parvifolia*	*L.* extinct
Populus pliotremuloides	*P. tremuloides*	*Sorbus* sp. nov.	*S. aucuparia*
Salix knowltonii	*S. lemmonii*	*Acer columbianum*	*A. glabrum*
Salix sp. nov.	*S. melanopsis*	*Acer middlegateii*	*A. saccharinum*
Salix wildcatensis	*S. lasiolepis*	*Acer oregonianum*	*A. macrophyllum*
Betula lacustris	*B. papyrifera*		

The taxa that have been found in the Middlegate but are not now known from the Purple Mountain flora are listed in Table 3.

Table 2. Species associated with *Abies scherrii* in only the Purple Mountain flora.

Fossil Species	Similar Living Species	Fossil Species	Similar Living Species
Salix sp. nov.	*S. nigra*	*Ceanothus leitchii*	*C. velutinus*
Castanopsis sonomensis	*C. chrysophylla*	*Rhamnus precalifornica*	*R. californica*
Holodiscus idahoensis	*H. glabrescens*	*Arbutus matthesii*	*A. menziesii*
Amorpha oklahomensis	*A. fruticosa*	*Leucothoe* sp. nov.	*L. davisiae*

TABLE 3. Species associated with *Abies scherrii* in only the Middlegate flora.

Fossil Species	Similar Living Species	Fossil Species	Similar Living Species
Pinus florissantii	*P. ponderosa*	*Crataegus middlegateii*	*C. chrysophylla*
Salix owyheeana	*S. hookeriana*	*Prunus morganensis*	*P. emarginata*
Salix hesperia	*S. lasiandra*	*Acer minor*	*A. negundo*
Alnus harneyana	*A. tenuifolia*	*Rhus alvordensis*	*R. glabra*
Betula vera	*B. lenta*	*Ceanothus precuneatus*	*C. cuneatus*
Quercus wislizenoides	*Q. wislizenii*	*Styrax middlegateii*	*S. californica*
Mahonia sp. nov.	*M. nervosa*	*Diospyros andersonae*	*D. virginiana*
Hydrangea bendireii	*H. aspera*	*Arbutus prexalapensis*	*A. arizonica*
Platanus paucidentata	*P. racemosa*	*Fraxinus millsiana*	*F. anomala*
Platanus dissecta	*P.* extinct	*Fraxinus coulteri*	*F. oregona*

The differences in composition are attributable to two factors. First, the Middlegate sample is larger (7,200 specimens) than that at Purple Mountain (1,200 specimens), so it would be expected to have more numerous species (50 vs. 35 taxa). Second, the somewhat greater age of the Middlegate (15–16 m.y.) as compared with Purple Mountain flora (13 m.y.) accounts for the more numerous exotic taxa (*Acer tyrrellii*, *Betula vera*, *Crataegus middlegatei*, *Diospyros andersonae*, *Hydrangea bendirei*, *Platanus dissecta*) in it. Nonetheless, it is noteworthy that the lists include many species which, in terms of their closest modern relatives, are associated frequently at the present time. Hence, the floristic differences are not as great as one might otherwise suppose. This becomes apparent if we compare the principal vegetation types that the modern species similar to the fossils represent, as well as other aspects of the paleoecology of these floras.

PALEOECOLOGY

VEGETATION

Broadleaved Evergreen Forest.—Fossil Santa Lucia fir (*Abies scherrii*) occurs in floras in which broadleaved sclerophylls are commonly dominant. *Quercus hannibalii*, which is similar to the living *Q. chrysolepis*, makes up 85% of all specimens in the Middlegate flora, and it also dominates several of the 10 florules in the Purple Mountain area. *Abies bracteata*, which is similar to the fossil *A. scherrii*, is regularly associated with a dominant *Quercus chrysolepis* sclerophyll community in areas of its optimum development. Among its more common associates that make up broadleaved evergreen forest that interfingers with patches of conifer forest in the higher Santa Lucia Mountains are *Arbutus menziesii*, *Lithocarpus densiflorus*, and *Quercus wislizenii*, all with close equivalents in the western Nevada floras. Many of their associates have analogues in the Miocene floras that have fossil Santa Lucia fir, notably *Acer negundo*,[3] *Acer macrophyllum*,[3] *Ceanothus cuneatus*, *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Platanus racemosa*,[3] *Rhamnus californica*, *Salix lasiandra*,[3] and *Salix melanopsis*.[3]

[3] Chiefly riparian.

Other taxa in these floras have their nearest relatives in sclerophyll vegetation in areas of summer rainfall, from southern Utah and Arizona to western Texas and southward into Mexico, notably *Acer grandidentatum*, *Arbutus arizonica*, *Cercocarpus paucidentatus*, *Fraxinus anomala*, *Fraxinus velutina*,[3] *Populus angustifolia*[3] (rare in So. Calif.), and *Robinia neomexicana*.

Mixed Conifer Forest.—The sclerophyll-dominated slopes and flats near the Miocene basins of plant accumulation were bordered by a mixed conifer forest dominated by *Sequoiadendron*, with associates of *Abies* (*concolor*, *magnifica-shastensis*),[4] *Picea* (*breweriana*, *polita*), *Pinus* (*ponderosa*), *Pseudotsuga* (*menziesii*), and *Chamaecyparis* (*lawsoniana*) among the common conifers. Their associates included fossil species of *Acer*, *Alnus*, *Amelanchier*, *Crataegus*, *Fraxinus*, *Holodiscus*, *Mahonia*, *Platanus*, *Prunus*, *Populus*, *Rosa*, *Salix*, *Sorbus*, and others, as listed above under COMPOSITION. In addition, each flora also has a few forest taxa that indicate summer rain, notably *Acer* (*grandidentatum*, *saccharinum*), *Betula* (*lenta*, *papyrifera*), *Diospyros* (*virginiana*), *Hydrangea* (*aspera*) and *Platanus* (cf. *occidentalis*). More numerous members of this alliance are in floras of similar age to the north in Oregon, or to the west in California. Their poorer representation in the Nevada floras is chiefly due to nearby terrain that produced local rainshadows over these basins.

The Miocene occurrence of *Abies scherrii* with dominant evergreen sclerophyllous vegetation, and with mixed conifer forest on bordering nearby slopes, parallels the occurrence of *A. bracteata* in the Santa Lucia Mountains today (Fig. 2). In this regard, it is noteworthy that *A. bracteata* inhabits steep terrain, living chiefly in sites where it is protected from fire by rocky bluffs and cliffs. In such sites it is well removed from areas where it might contribute to a fossil record. The question may thus be posed: Is the rarity of *A. scherrii* in the fossil record to be attributed to its preference for well drained, rocky sites scattered in the ecotone between mixed conifer forest and broadleaved sclerophyll vegetation?

There are important differences betwen the Miocene and the modern communities. These can be understood if we first reconstruct the physical setting of the Miocene community.

CLIMATE

Santa Lucia fir ranges through the canyon live oak-tan oak-madrone sclerophyll vegetation, reaching up into the mixed conifer forest in the Santa Lucia Mountains at levels from 4,000 to 5,000 feet. This is shown by its occurrence with *Pinus lambertiana*, *P. ponderosa*, and *P. coulteri* at or near Cone Peak, with *Calocedrus decurrens* and *Pinus lambertiana* at or near Junipero Serra Peak, and with *Calocedrus decurrens*, *Pinus ponderosa*, and *P. coulteri* at South Ventana Cone. With certain qualifications noted below, thermal conditions in the ecotone from conifer forest to broadleaved sclerophyll forest may be considered to approximate Miocene temperatures. Temperatures can be determined from records at stations in the Sierra Nevada where mixed conifer forest interfingers with

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[4] Species in parenthesis are living plants that seem most nearly related to the fossils.

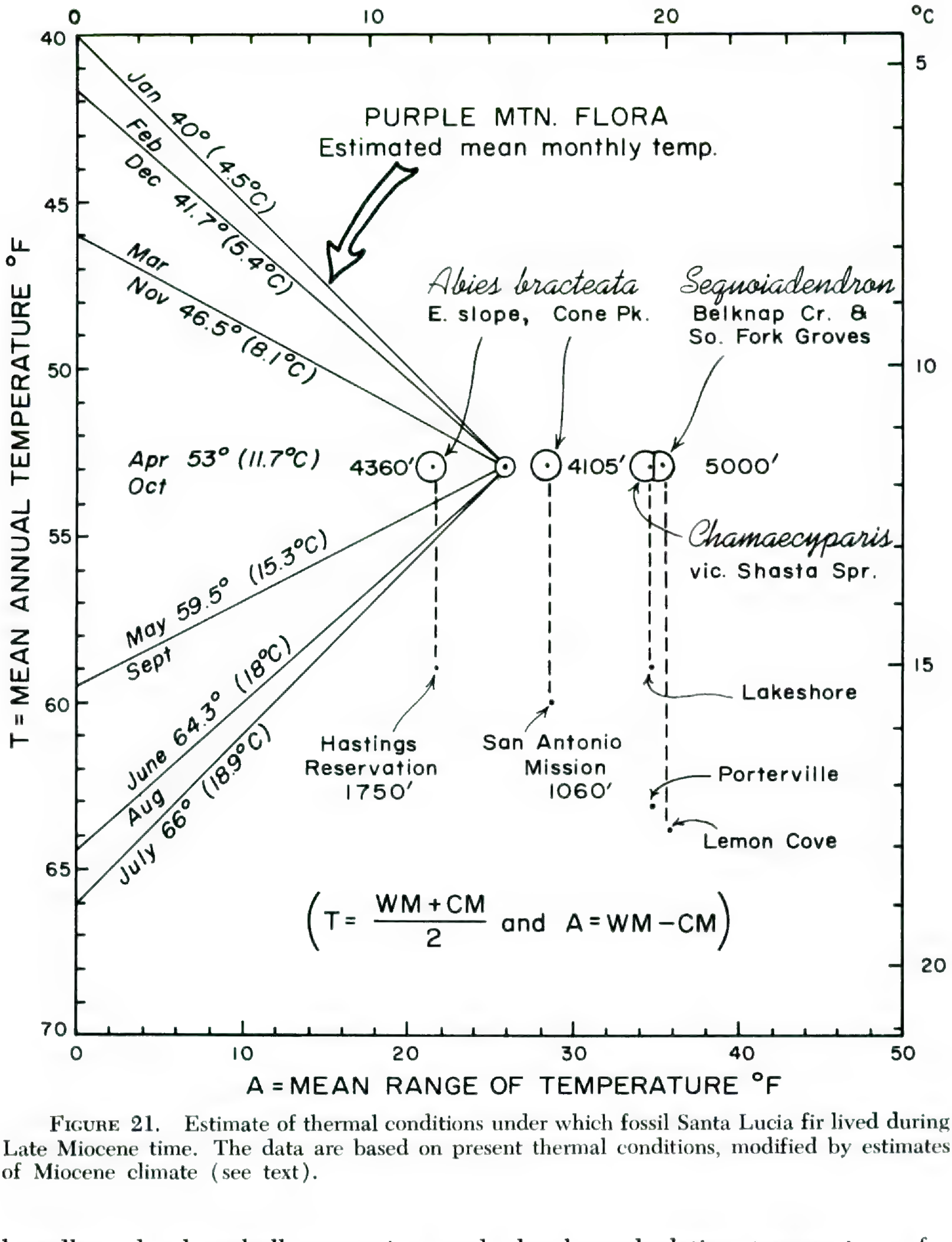

FIGURE 21. Estimate of thermal conditions under which fossil Santa Lucia fir lived during Late Miocene time. The data are based on present thermal conditions, modified by estimates of Miocene climate (see text).

broadleaved sclerophyll vegetation, and also by calculating temperatures for specific sites from stations in the adjacent lowlands to the west. Temperatures in the area of Santa Lucia fir can be estimated from meterological records at stations in the nearby region to the east and north.

The latter method is illustrated in Figure 21. Temperatures for two stations with *Sequoiadendron*, Belknap Creek (4,800 ft.) and South Fork Grove (5,000 ft.) were calculated from temperatures at Lemon Cove (alt. 513 ft., $T = 63.9°$, $A = 35.7°F$) and Porterville (alt. 393 ft., $T = 63.2°$, $A = 34.6°F$), using a lapse rate

of 2.5°F per 1,000 feet.[5] Figure 21 shows that they live under a mean temperature of ~ 53°F. A similar result is suggested by data used to estimate conditions where Santa Lucia fir overlaps members of the Sierra mixed conifer forest at altitudes between 4,000 and 5,000 feet. There the stations selected are Hastings Reservation (alt. 1,750 feet, $T = 59.1°$, $A = 21.5°F$) and San Antonio Mission (alt. 1,060 ft., $T = 60.2°$, $A = 28.4°F$), utilizing a lapse rate of 2.5°F per 1,000 feet. The mean January and July temperatures estimated for the east slope of Cone Peak at 4,200 feet (see Fig. 21) are similar to those recorded there by Talley (1974) for those months in 1971. Significantly, this was a year in which temperatures at lowland stations in Salinas Valley to the east were close to the 30-year norm. Figure 21 also shows estimated temperature for the Shasta Springs area, where *Chamaecyparis* is in the ecotone between mixed conifer forest and broadleaved sclerophyll vegetation. The temperature was calculated from the records at Mt. Shasta City (alt. 3,544 ft., $T = 49.9°$, $A = 34.7°F$) and Lakeshore (alt. 1,075 ft., $T = 58.9°$, $A = 34.8°F$).

The range of temperature (A) in the Miocene was more nearly like that now in the forest-sclerophyll ecotone in the Coast Ranges than in the Sierra Nevada. This seems likely inasmuch as the fossil floras with *Abies scherrii* (cf. *bracteata*) all have a few taxa that live chiefly on the coastward slopes, notably *Picea* (cf. *breweriana*), *Chamaecyparis* (cf. *lawsoniana*), and *Castanopsis* (cf. *chrysophylla*) in northwestern California,[6] or are found in the coastal strip farther south, as exemplified by *Cercocarpus* (cf. *blancheae*), *Lyonothamnus* and *Mahonia* (cf. *insularis*). Furthermore, with some summer rainfall over the region—as compared with clear, cloudless summer skies today—the cloud deck would reduce the high summer temperatures. Also, *Sequoia* (*sempervirens*) was then living on the coastward slope of the Sierra Nevada (Condit, 1944) 90 miles west of the Purple Mountain flora. Its occurrence there together with *Chamaecyparis*, *Lithocarpus*, *Persea*, and *Umbellularia* clearly implies a low range of temperature. By inference, comparable conditions must have extended inland since the northern Sierra was then only a low ridge without significant relief (Durrell, 1966: 192–195; Axelrod, 1956). Since the fossil floras with *Abies* (*bracteata*) represent an environment like that now in the ecotone between broadleaved sclerophyll and mixed conifer forest, thermal conditions there were approximately as shown in Fig. 21: mean annual temperature, 53°F; mean range of temperature, 26°F; mean July temperature, 66°F; and mean January temperature 40°F. From these data it is estimated that the Miocene ecotone had an effective temperature (ET) or warmth (W) of 55.7°F, or 158 days with a mean temperature above 55.7°F.

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[5] Temperature normally decreases as altitude increases. In air free from the surface, the standard lapse rate is –3.6°F/1,000 ft. But close to the ground, heat is supplied to the overlying air during the day, so air temperatures measured in the instrument shelter record conditions warmer than those in free air. This "ground effect" thus reduced the lapse rate, and gives a "terrestrial" lapse rate that approximates 3.0°F/1,000 ft. under normal conditions (H. P. Bailey, written communication, Jan., 1975).

[6] The scrub form, var. *minor*, occurs to the south Coast Ranges. The tree form var. *chrysophylla* has a relict occurrence in the Sierra Nevada near Pino Grande, Placer County, in the lower part of the mixed conifer forest where it is associated with *Quercus chrysolepsis*, *Lithocarpus densiflorus*, and *Arbutus menziesii*.

The temperateness index was *M* 57, and about 4% of the hours of the year had frost (see Bailey, 1960, 1964).

It is emphasized that Miocene thermal conditions differed from present ones in two important ways. *First*, winters must have been more mild because ice caps were not yet in existence and hence cold and freezing conditions (like the winter ice storm of 1974) were not yet present. *Second*, in view of warmer Miocene seas, summers were moist and warm, high evaporation such as exists today could not have been present, and hence summer temperatures were more moderate than those of today. The temperatures estimated above must therefore be *extreme* for the Late Miocene. Clearly, temperatures were more equable than those now in the ecotone from mixed conifer forest to broadleaved sclerophyll vegetation at altitudes near 4,000–5,000 feet in the Santa Lucia Mountains where *Abies bracteata* lives today.

Precipitation in the mixed conifer–evergreen sclerophyll forest ecotone near 4,000 feet in the Santa Lucia Mountains is about 35–40 inches, distributed chiefly in the winter season as rain, and occasionally as light snow. As noted earlier, there was some summer rainfall over western Nevada during the Late Miocene, probably amounting to several inches for the summer season. The minimum rainfall required to support the flora can be estimated also from the temperatures suggested above for the Miocene ecotone. Using a mean temperature (*T*) of 53°F and a range of temperature (*A*) of 26°F, the Water Need (*N*), which is based on the exponential relation between temperature and moisture (see Bailey, 1958), calls for a minimum precipitation of about 35 inches, including that of the summer season.

ALTITUDE

The general altitude of the lake basins in western Nevada that were situated in the ecotone between mixed conifer forest and broadleaved sclerophyll vegetation was estimated earlier to be near 2,000 to 2,500 feet. This was based on the general relations of vegetation and climate, and on evidence that a major rain-shadow like that of the present had not yet developed (Axelrod, 1956).

Altitude can also be estimated by comparing thermal conditions in the Miocene of Nevada with that at sea level to the west, and interpolating altitude from the difference in mean temperature (Axelrod, 1965, 1968). As estimated above, thermal conditions in the forest-sclerophyll ecotone were approximately *T* 53°F and *A* 26°F. During the Late Miocene the coastal strip had a mean temperature near 60° to 61°F as judged from the slightly younger Neroly flora of western California that resembles vegetation in coastal Virginia (Condit, 1938). Temperatures were somewhat warmer during the Middle Miocene (~ 15 m.y.) as judged from the Temblor flora near Coalinga (Rennie, 1972) which is situated 145 miles southeast of the Neroly flora. It shows relationship to vegetation in coastal North Carolina, where mean temperature is 62° to 63°F. Assuming a Late Miocene terrestrial lapse rate of 3.0°F per 1,000 feet (or 1° = 333 feet), a difference in mean temperature of approximately 7°F–8°F between the Purple Mountain flora and the Miocene floras at sea level implies a minimum altitude of about 2,300–2,600 feet. Realizing that this is an estimate, it seems likely that the Purple

Mountain flora had an altitude near 2,500 feet. This agrees closely with earlier estimates for the Fallon and Chloropagus floras of the nearby region, estimates based on very different lines of reasoning (Axelrod, 1956).

Post-Miocene Changes

The mixed conifer forest that inhabited cooler, moister slopes and valleys bordering the sclerophyll-dominated basins was richer than the modern descendant vegetation. It included conifers related to those that are now restricted in area, notably *Picea breweriana* and *Chamaecyparis lawsoniana* that are confined to northwestern California, *Sequoiadendron giganteum* which lives in the central and southern Sierra Nevada, as well as *Abies magnifica* and *Pinus monticola* that now occur in subalpine sites in the Sierra Nevada well removed from Santa Lucia fir today. Similar relations are displayed by the broadleaved sclerophyll vegetation, for the Miocene community included species similar to those now in coastal southern California, notably species of *Cercocarpus*, *Lyonothamnus*, and *Mahonia*. Furthermore, both vegetation zones had a few species related to those now in areas with summer rain.

The emergence of modern communities of lower diversity and more restricted area is due to the gradual development of new moisture-thermal conditions during the Pliocene which culminated in the appearance of summer-dry mediterranean climate in the middle and late Quaternary. Increasing summer drought has resulted in progressively greater water stress during the critical period of seedling germination, growth, and establishment (Axelrod, 1976). Hence, taxa that were unable to adapt to these new conditions in the lower part of the mixed conifer forest near broadleaved evergreen sclerophyll vegetation were gradually confined to areas in which they could reproduce successfully. The regular occurrence in the Miocene of such "subalpine" species as *Abies* (*magnifica*), *Pinus* (*monticola*), *Tsuga* (*mertensiana*) and *Populus* (*tremuloides*) with mixed conifer forest taxa as *Abies* (*concolor*), *Pinus* (*ponderosa*), *Calocedrus* (*decurrens*), and *Sequoiadendron* (*giganteum*), and with broadleaved sclerophylls as *Quercus* (*chrysolepis*, *wislizenii*), *Castanopsis* (*chrysophylla*), *Lithocarpus* (*densiflorus*), *Arbutus* (*menziesii*), in the *same* fossil flora, is symptomatic of the nature of the post-Miocene changes in community composition that were due to changing climate, and chiefly to increased water deficit in the summer season. Its effect can be summarized in terms of the modifications that appear to account for the distributions of taxa whose Miocene relatives were associated with fossil Santa Lucia fir, and which now define the segregate communities of lower diversity that are confined to more local areas.

Sierra redwood (*Sequoiadendron*), which is restricted to the central and southern Sierra Nevada, probably entered the range following the Late Miocene as rainfall decreased and as conditions became sunnier there. *Sequoiadendron* is now known from the Middle Pliocene Mount Reba flora (7 m.y.), Alpine County. The site is at wind timberline, *above* a subalpine forest of *Abies magnifica*, *Pinus monticola*, and *Tsuga mertensiana*. The Mt. Reba flora is dominated by broadleaved sclerophyllous evergreens, as shown by the abundance of specimens of *Quercus* (*chrysolepis*), *Lithocarpus* (*densiflora*), and *Cupressus* (*cashmeriana*).

Pseudotsuga (*menziesii*) is also common, and probably formed rich stands on nearby slopes much as it does today at levels near 2,000–2,500 feet in the lower foothills of the range. A few scraps of other conifers are present, notably *Abies* (*concolor*) and *Sequoiadendron*. The community shifted to lower levels as colder climates developed as the range was elevated later in the Pliocene and during the Quaternary.

Reasons for the present absence of *Sequoiadendron* in the Sierra Nevada north of the American River drainage (Placer County) are not clear. However, the region receives much higher rainfall, and a number of taxa that are typical of forests in the Coast Ranges occur in the northern Sierra Nevada. This gives to the mixed conifer forest of that area a denser, richer understory of shrubs and small trees than in the Sierra farther south. As a result, relatively less light falls on the forest floor, and conditions are therefore unfavorable for taxa that are light demanding, especially in the seedling stage. That Sierra redwood seedlings thrive best under conditions of ample light is apparent from the heavy reproduction that occurs about the margin of moist meadows in the southern Sierra today, as at Balch Park in Tulare County, east of Exeter. This agrees with the experimental studies by Stark (1968a) who noted "growth in full sunlight was superior to that in any shady forest" (p. 91) and that "healthy . . . seedlings grow best in full sunlight" p. 92). Stark (1968b: 276) also noted that the failure of trees to spread and expand their present range is the result of fire-suppression over the past decades, with the accumulation of a deeper-than-normal litter, as well as an increase in growth of understory shrubs and trees, and hence an increase also of shade within the forest.

One other point is to be noted in terms of the need of *Sequoiadendron* seedlings for ample light. Sierra redwood occurs at numerous sites in the Miocene of Nevada and also at a locality (Trapper Creek) in southeastern Idaho. However, it has not been recorded in any of the Miocene floras that are scattered widely in Oregon, Washington, and western Idaho. The floras of that region are richer in taxa than in the area to the south chiefly because of the higher precipitation there. Mesic conifers (*Cephalotaxus*, *Ginkgo*, *Glyptostrobus*, *Metasequoia*, *Sequoia*, *Taxodium*) are present in most of these floras, and deciduous hardwoods are especially abundant together with some associated broadleaved evergreens. But in the Miocene floras to the south, mesic conifers are rare to absent, deciduous hardwoods have a poorer representation, and sclerophyllous taxa increase in diversity and abundance. These relations imply climate was drier and sunnier to the south, which is consistent with the composition of the Miocene floras in the Mohave region where live oak woodland and thorn scrub are wholly dominant (Axelrod, 1958). The general distribution of *Sequoiadendron* during the Miocene is therefore consistent with conditions that it seems to require for best reproduction—ample light and sufficient moisture during the critical stage of seedling establishment.

Taxa that are often considered "subalpine indicators," notably *Abies magnifica*, *Picea breweriana*, *Pinus monticola*, *Tsuga mertensiana*, *Populus tremuloides*, and others, have close relatives in the Miocene floras of Nevada where they occur with sclerophyllous taxa and fossil Santa Lucia fir. Since geologic evidence shows

that these plants lived in terrains of low relief, and since "subalpine" species are sufficiently abundant numerically to form codominants of some of the fossil floras, they must have lived near at hand (Axelrod, 1976). This means they were regular members of the mixed conifer forest. Such an occurrence is consistent with the presence of most of their living descendants in mixed conifer forest in areas to the north, where there is more rainfall in summer, a longer precipitation season, and a lower evaporation rate (Axelrod, 1976). The taxa that are now confined to subalpine forest in the Sierra evidently were restricted to that zone as dry summer, montane mediterranean-type climate spread during the later interglacial ages. Thus, the distinctness of the modern subalpine (or pure conifer) forest in the Sierra Nevada is due to the restriction of its taxa to this higher, cooler zone where the effect of high evaporation (= water deficit = water stress) is less than in the mixed conifer forest at lower levels, a forest from which they are now largely excluded.

The confinement of *Abies bracteata* to the Santa Lucia Mountains seems consistent with its mild climate and lower evaporation rate in summer as compared with the Sierra where many of its former associates occur. In this regard, the forested parts of the outer Coast Ranges have lower summer temperature and milder winters than comparable parts of the Sierra (Fig. 21). Thus, Santa Lucia fir may have been eliminated from the Sierra Nevada, where it probably occurred during the Pliocene, by the high evaporation rate in summer which was inimical to seedling establishment. A second factor was increasing winter cold with accompanying snow and ice. That it would have had a disastrous effect on the trees at higher levels in the ecotone between mixed evergreen forest and mixed conifer forest may be inferred from the severe damage inflicted by the snow and ice storm on Santa Lucia fir during the winter of 1974, which resulted in numerous broken tops (with cones) and limbs (oral communication, S. Talley, 1974). Similar damage was inflicted on its broadleaved evergreen associates, notably *Arbutus menziesii*, *Lithocarpus densiflorus*, *Quercus chrysolepis*, and *Q. wislizenii*. On this basis we may infer that conditions probably were too severe for *A. bracteata* in the Sierra Nevada during the glacial ages. In this regard, its present absence from the Coast Ranges farther north may reflect the more severe winters there, for the frequency of snow increases northward and the mean January temperature rapidly falls below 40°F, which appears to be near the minimum for the species today (Fig. 21).

The present absence of Santa Lucia fir farther south in the Coast Ranges may reflect a recent restriction in range. It may possibly have been eliminated there by the xerothermic periods of the later Quaternary (Axelrod, 1966: 42–55). This seems consistent with the paucity of conifer forest taxa in the isolated areas where forest now occurs in the central Coast Ranges (Axelrod, 1976). Altitudes in these areas, whether in the Santa Cruz or Santa Lucia mountains or the interior Diablo and La Panza ranges, are relatively low and the forest has only one or two species. However, in the higher north Coast Ranges (north of Clear Lake), the Sierra Nevada, the Transverse Ranges and Peninsular Ranges of southern California, the forest has mixed stands of several conifers. It seems

likely that a warm dry xerothermic period would have eliminated many forest taxa from the central Coast Ranges simply because terrain was not sufficiently high to provide cool, moist sites for them, and hence they disappeared because drought stress militated against successful reproduction.

That richer, more diverse forests were in the region earlier is shown by the occurrence of *Calocedrus decurrens* and *Pinus lambertiana* in the Santa Cruz Mountains during the Plio-Pleistocene transition (Dorf, 1930: 18). This may also be inferred from the occurrence of a rich mixed conifer forest on the valley floor near San Jacinto in southern California (Axelrod, 1966), a region now semi-desert. The occurrence of *Sequoia sempervirens* and *Pseudotsuga menziesii* along the Santa Barbara coast during the late Quaternary (Axelrod, 1967: 295–296), and the present relict stand of mixed evergreen forest (*Arbutus menziesii, Quercus chrysolepsis, Lithocarpus densiflorus*) in the nearby summit section of the Santa Ynez Range at San Marcos Pass also provide hints of the nature of the forests that probably inhabited the central Coast Ranges during the cooler, moister phases of the Quaternary.

LITERATURE CITED

AXELROD, D. I. 1956. Mio-Pliocene floras from west-central Nevada. Univ. Calif. Publ. Geol. Sci. 33: 1–316.

———. 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. (Lancaster) 24: 433–509.

———. 1965. A method of determining the altitudes of Tertiary floras. Paleobotanist 14: 144–171.

———. 1966. The Pleistocene Soboba flora of southern California. Univ. Calif. Publ. Geol. Sci. 60: 1–108.

———. 1967. Geologic history of the Californian insular flora. Pp. 267–315, *in* R. N. Philbrick (editor), Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Bot. Garden, Santa Barbara, Calif.

———. 1968. Tertiary floras and topographic history of the Snake River Basin, Idaho. Bull. Geol. Soc. Amer. 79: 713–734.

———. 1976. History of the conifer forests, California and Nevada. Univ. Calif. Publ. Bot. 60: 1–62.

BAILEY, H. P. 1958. A simple moisture index based upon a primary law of evaporation. Geogr. Ann. Svenska Sällsk. Antropol. 40: 196–215.

———. 1960. A method of determining the warmth and temperateness of climate. Geogr. Ann. Svenska Sällsk. Antropol. 42: 1–16.

———. 1964. Toward a unified concept of the temperate climate. Geogr. Rev. (New York) 54: 516–545.

BONHAM, H. F. 1969. Geology and mineral deposits of Washoe and Storey Counties, Nevada. Bull. Nevada Bur. Mines 70: 1–140.

CHANEY, R. W. & D. I. AXELROD. 1959. Miocene floras of the Columbia Plateau. Publ. Carnegie Inst. Wash. 516: 1–237.

CONDIT, C. 1938. The San Pablo flora of west central California. Publ. Carnegie Inst. Wash. 476: 217–268.

———. 1944. The Remington Hill flora (California). Publ. Carnegie Inst. Wash. 553:21–55.

DORF, E. 1930. Pliocene floras of California. Publ. Carnegie Inst. Wash. 412:1–108.

DURRELL, C. 1966. Tertiary and Quaternary geology of the northern Sierra Nevada. Bull. Calif. Div. Mines Geol. 190: 185–197.

GRIFFIN, J. R. & W. B. CRITCHFIELD. 1972. The distribution of forest trees in California. U.S.D.A. Forest Serv. Res. Pap. PSW 82.

KNOWLTON, F. H. 1923. Fossil plants from the Tertiary lake-beds of south-central Colorado. Profess. Pap. U.S. Geol. Surv. 131: 183–197.

LIU, TANG-SHUI. 1971. A monograph of the genus *Abies*. Dept. Forest., Coll. Agric., Nat. Taiwan Univ., Taipei, Taiwan. 608 pp.

MacGinitie, H. D. 1953. Fossil plants of the Florissant beds, Colorado. Publ. Carnegie Inst. Wash. 599: 1–188.
Mason, H. L. 1927. Fossil records of some west American conifers. Publ. Carnegie Inst. Wash. 346: 139–158.
Rennie, K. M. 1972. The Miocene Temblor flora of west central California. MS thesis, Univ. California, Davis. 106 pp.
Rose, R. L. 1969. Geology of parts of the Wadsworth and Churchill Butte quadrangles, Nevada. Bull. Nevada Bur. Mines 71: 7–27.
Stark, N. 1968a. The environmental tolerance of the seedling stage of *Sequoiadendron giganteum*. Amer. Midl. Naturalist 80: 84–95.
———. 1968b. Seed ecology of *Sequoiadendron giganteum*. Madroño 19: 267–277.
Talley, S. N. 1974. The ecology of Santa Lucia fir (*Abies bracteata*), a narrow endemic of California. PhD thesis, Duke Univ., North Carolina. 208 pp.

STUDIES IN BIGNONIACEAE 18: NOTES ON S. MOORE'S MATO GROSSO BIGNONIACEAE[1]

ALWYN H. GENTRY[2]

ABSTRACT

The 16 species of Bignoniaceae described by Moore from his own and Robert's Mato Grosso collections are identified. Three new combinations based on Moore's species are made.

In preparation for the treatment of Bignoniaceae for Flora Neotropica I am attempting to identify the numerous, unaccounted-for species described in *Bignonia* prior to 1900. Spencer Moore's Mato Grosso Bignoniaceae are among the most important of these. In 1895 Moore (1895) described 14 new species of Bignoniaceae collected during the Percy Sladen Mato Grosso Expedition of 1891–1892. Later (Moore 1904, 1907) he described two additional species of Bignoniaceae from the same area. Moore's species, described mostly in the genus *Bignonia*, have never been reinterpreted nor identified with known species of Bignoniaceae. The holotypes of Moore's collections are maintained in the herbarium of the British Museum of Natural History (BM); there are also partial sets at NY and MO. Through the kindness of the curator of the British Museum's Botany Department, I have been able to examine the holotypes of these plants. This paper identifies them to genus and species and proposes the three necessary new combinations based on Moore's names. Moore's other 13 species are reduced to synonymy.

The nomenclatural significance of Moore's species is due to the fact that they were published just prior to Bureau & Schumann's (1896–1897) treatment of Bignoniaceae for Flora Brasiliensis. Published too late for inclusion in Flora Brasiliensis, these names have priority over those published in that work and subsequently. A few of Moore's plants were identified in the Flora Brasiliensis on the basis of the distributed specimens, however. The following 16 species of Bignoniaceae were described by Moore.

1. **Bignonia rubescens** S. Moore is *Arrabidaea chica* (H. & B.) Verl. (based on *B. chica* H.&B., Pl. Aeq. 1: 107, *tab. 31.* 1808.) as noted by Bureau & Schumann (as *B. erubescens*).

2. **Bignonia tomentella** S. Moore is *Arrabidaea pubescens* (L.) A. Gentry (based on *B. pubescens* L., Sp. Pl., ed. 2, 2: 870. 1763.) and falls into the synonymy of that species.

3. **Bignonia grewioides** S. Moore is *Arrabidaea fagoides* (Cham.) Bur. (based on *B. fagoides* Cham., Linnaea 7: 680. 1832.) and becomes a synonym of that species which is itself uncomfortably close to *A. platyphylla* DC.

4. **Bignonia melioides** S. Moore is *Pleonotoma brittonii* Rusby (Bull. Torrey Bot. Club 27: 72. 1900.) and Moore's name is older. The new combination **Pleono-**

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toma melioides (S. Moore) A. Gentry (based on *B. melioides* S. Moore, Trans. Linn. Soc. London, Bot. 4: 414. 1895.) is necessary.

5. **Bignonia caudigera** S. Moore is *Arrabidaea coleocalyx* Bur. & K. Schum. (Fl. Bras. 8(2): 35. 1896.) and Moore's name is older. The new combination **Arrabidaea caudigera** (S. Moore) A. Gentry (based on *B. caudigera* S. Moore, Trans. Linn. Soc. London, Bot. 4: 415. 1895.) is necessary for this well-known species.

6. **Bignonia modesta** S. Moore is a species of *Stizophyllum* and Sandwith has annotated the type as *S. riparium* (H.B.K.) Sandw. sensu lato. Moore's plant differs from other specimens of *S. riparium* seen by me in its smaller serrulate leaflets. It differs from *S. perforatum* (Cham.) Miers in less noticeable pubescence, smaller serrulate leaflets, and especially the smaller uninflated calyx. The pink flower color agrees with *S. perforatum* or *S. inaequilaterum* Bur. & K. Schum. but not *S. riparium* sensu stricto. Species limits in *Stizophyllum* are hazy at best and only additional collections from Mato Grosso can tell whether *B. modesta* should be regarded as specifically distinct. For the present it may be tentatively included under *S. riparium*.

7. **Macfadyena riparia** S. Moore is a form of *Phryganocydia corymbosa* (Vent.) Bur. ex K. Schum. (based on *Spathodea corymbosa* Vent., Choix *tab. 40.* 1807.) and becomes a synonym of that species. The predominantly simple leaves of Moore's plant are insufficient grounds for species segregation.

8. **Macfadyena bipinnata** S. Moore is an otherwise undescribed species of *Memora*. The new combination **Memora bipinnata** (S. Moore) A. Gentry (based on *Macfadyena bipinnata* S. Moore, Trans. Linn. Soc. London, Bot. 4: 418. 1895.) is necessary for this plant which is amply distinguished by its softly puberulous leaves with relatively large leaflets and lack of foliaceous pseudostipules. A second collection of this species is *Prance et al. 18906* from the Chapada dos Guimarães, cerrado behind Colegio de Buriti, Mato Grosso. It differs from the type in simply pinnate leaves but is otherwise a good match. *Memora axillaris* Bur. & K. Schum. (a simply pinnate leaved species with foliaceous pseudostipules and a very different pubesence texture) may be the closest relative of *M. bipinnata*; *M. axillaris* is younger than Moore's basionym and would become a junior synonym should the two be united.

9. **Macfadyena pubescens** S. Moore is *Macfadyena mollis* (Sonder) Seem. (based on *Spathodea mollis* Sonder, Linnaea 22: 561. 1849.) which is itself synonymous with *Macfadyena hispida* (DC.) Seem. (based on *Spathodea hispida* DC., Prodr. 9: 205. 1845.). Seemann (1863) followed by Fabris (1965) separated *M. mollis* and *M. hispida* on what I consider tenuous grounds. In either case Moore's plant falls into synonymy.

10. **Adenocalymma croceum** S. Moore is *Adenocalymma bracteolatum* DC. (Prodr. 9: 200. 1845.) and becomes a synonym of that species. The only known fruiting collection of *A. bracteolatum* was collected by Roberts and identified by Moore with his *A. croceum*. This collection contains two immature capsules which

are oblong, obtuse at base and apex, 13–14 cm long, 2–2.2 cm wide, minutely lepidote, otherwise glabrous, drying dark with numerous pale lenticels, and somewhat flattened in drying but probably subterete when fresh. The unwinged fruit of *A. bracteolatum* proves that the more widespread and closely related *Adenocalymma* with winged fruits is not synonymous with this species and must be known as *A. purpurascens* Rusby (see Gentry, 1976). The ovary of Moore's collection agrees with that of the type of *A. bracteolatum* in being linear-oblong without lateral ridges, unlike the 4-ridged ovary of *A. purpurascens*.

11. **Anemopaegma brevipes** S. Moore is closely related to the earlier *A. flavum* Morong (Ann. New York Acad. Sci. 7: 188. 1893.) on account of its glabrous corolla tube and foliaceous pseudostipules. It appears to be distinct by its much denser pubescence, especially on the lower leaflet surface. I would tentatively assign a second collection to *A. brevipes*. This is *Pirres & Leite 14692* (MO) from Roraima Territory. Its only noticeable difference is a more strongly bracteate less pubescent inflorescence, although its geographic disjunction is rather striking. While *Anemopaegma chrysoleucum* (H. B. K.) Sandw., *A. flavum*, and *A. brevipes* are clearly related and form a series subdivided mostly by increasing pubescence, they seem to be specifically distinct. The New York "isotype" of *A. brevipes* is actually *A. flavum*, however. *Anemopaegma bifarium* Bur. & K. Schum. (Fl. Bras. 8(2): 124. 1896.) is based on Moore's collection, but Moore's name is older.

12. **Anemopaegma decorum** S. Moore is *Clytostoma decorum* Bur. & K. Schum. (Fl. Bras. 8(2): 1896.). Although Bureau & Schumann had not seen Moore's description, they saw a duplicate of his collection and redescribed the species in its correct genus. Moore's description is older than Bureau & Schumann's but *C. decorum* Bur. & K. Schum. blocks a combination in *Clytostoma* based on *A. decorum* S. Moore.

13. **Anemopaegma sylvestre** S. Moore is *Anemopaegma flavum* Morong (Ann. New York Acad. Sci. 7: 188. 1893.) and becomes a synonym of the latter.

14. **Tabebuia chapadensis** S. Moore is *Arrabidaea corallina* (Jacq.) Sandw. (based on *Bignonia corallina* Jacq., Fragm. Bot. 37, *tab. 42, fig. 1.* 1800–1809.) and has already been placed in the synonymy of that species (Gentry, 1973).

15. **Cremastus sanctae-annae** S. Moore (1904) is *Arrabidaea sceptrum* (Cham.) Sandw. (based on *Bignonia sceptrum* Cham., Linnaea 7: 710. 1832.). Sandwith (1968) suggested that *C. sanctae-annae* was probably a large-calyx form of *A. pulchra* (Cham.) Sandw., noting especially the agreement of its open pyramidal inflorescence with that of *A. pulchra*. I am hard pressed to distinguish *A. pulchra* from *A. sceptrum*; certainly the latter's inflorescence shows every kind of gradation from open to condensed. If *A. pulchra* is to be separated from *A. sceptrum*, its smaller calyx is the key character and the large calyx of *C. sanctae-annae* clearly allies it with the latter.

16. **Jacaranda robertii** S. Moore (1907) proves to be *J. decurrens* Cham. contrary to my earlier (Gentry, 1974) interpretation. The BM holotype of *J. robertii* (*Roberts 675*) is completely different from the MO "isotype" with the same col-

lection number. The holotype is clearly *J. decurrens*. The "isotype" is an undescribed species mixed with corollas of *J. decurrens*. The numerous discrepancies I previously noted between the MO specimen of *Roberts 675* and Moore's description are thus explained: except for the corollas we were looking at two quite unrelated plants. The MO specimen of *Roberts 675* has only vegetative parts, calyces, and very immature fruits of the new species, inadequate for its description at the present time.

Literature Cited

Bureau, E. & K. Schumann. 1896–1897. Bignoniaceae. *In* C. F. P. Martius (editor), Flora Brasiliensis 8 (2): 1–452.

Fabris, H. A. 1965. Bignoniaceae in Flora Argentina. Revista Mus. La Plata, Secc. Bot. 9: 273–419.

Gentry, A. H. 1973. Bignoniaceae. *In* R. E. Woodson, Jr. & R. W. Schery. Flora of Panama. Ann. Missouri Bot. Gard. 60: 781–977.

———. 1974. Studies in Bignoniaceae 12: New or noteworthy species of South American Bignoniaceae. Ann. Missouri Bot. Gard. 61: 872–885.

———. 1976. Studies in Bignoniaceae 19: Generic mergers and new species of South American Bignoniaceae. Ann. Missouri Bot. Gard. 63: 46–80.

Moore, S. 1895. The phanerogamic botany of the Mato Grosso Expedition 1891–92. Trans. Linn. Soc. London, Bot. 4: 265–516.

———. 1904. Mons. A. Robert's Mato Grosso Plants—I. J. Bot. 42: 106–107.

———. 1907. Note on some South American plants. J. Bot. 45: 404–406.

Sandwith, N. Y. 1968. Notes on Bignoniaceae XXIX: *Arrabidaea* in Martius's Flora Brasiliensis and subsequently. Kew Bull. 22: 403–420.

Seeman, B. 1863. Revision of the natural order Bignoniaceae. *Spathodea*. J. Bot. 1: 225–228.

STUDIES IN BIGNONIACEAE 19: GENERIC MERGERS AND NEW SPECIES OF SOUTH AMERICAN BIGNONIACEAE[1]

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ABSTRACT

Preparation of the treatment of Bignoniaceae for *Flora de Venezuela* and field work in Venezuela, Colombia, Ecuador, and Brazil have turned up several novelties and some taxonomic problems. In this paper the *Adenocalymma apurense*, *A. bracteolatum*, and *Amphilophium paniculatum* complexes in Venezuela are reinterpreted necessitating one new variety, one new combination, and resurrection of two previously synonymized species. *Anemopaegma villosum*, *Arrabidaea prancei*, *Cuspidaria subincana*, *Haplolophium rodriguesii*, *Mansoa onohualcoides*, *Memora aspericarpa*, *M. tanaeciicarpa*, *Tanaecium apiculatum*, *Tynnanthus villosus*, *Anemopaegma alatum*, and *A. patelliforme* are described as new. Seven generic mergers necessitating a total of nine new combinations are proposed: *Onohualcoa* to *Mansoa*, *Pseudopaegma* to *Anemopaegma*, *Sanhilaria* to *Paragonia*, *Nestoria* and *Kuhlmannia* to *Pleonotoma*, *Roseodendron* to *Tabebuia*, and *Xerotecoma* to *Godmania*. An eighth generic merger—*Distictella* with *Distictis*—is rejected, but a new combination is needed for one species which is transferred to *Distictis*.

Adenocalymma apurense (H.B.K.) Sandw. and relatives.

As previously interpreted (Gentry, 1974a), *A. apurense* (including *A. inundatum* and *A. calderonii*) is a polymorphic widespread species ranging from Mexico to Para, Brazil. Additional collections of this complex indicate that it is even more polymorphic than previously supposed. The *A. apurense* complex consists of at least three distinct entities which deserve formal taxonomic recognition. Each of these three entities, virtually indistinguishable on the basis of vegetative and floral characteristics, has a distinctive fruit.

A form with winged seeds and non-splitting capsule valves occurs from Mexico to northern Colombia and Venezuela and has been variously known as *A. inundatum* Mart. ex DC., *A. hintonii* Sandw. and *A. calderonii* (Standl.) Seib. The other two forms have wingless seeds and are restricted to South America. One, with non-splitting capsule valves and more coriaceous leaflets, has been known as *A. inundatum* var. *surinamense*. This form occurs from the upper Orinoco through the Guianas to Para, Brazil. I follow Sandwith in regarding it as not specifically distinct from the northern form with winged seeds. The third entity has wingless seeds and a shorter almost globose capsule with each valve splitting in half at maturity, i.e., effectively 4-valved. Although these three entities would not warrant any kind of taxonomic recognition on the basis of floral or vegetative characteristics, the 4-valved form can also be distinguished from the other two forms by its shorter (1–2 mm long) more square-ended ovary and is probably specifically distinct.

The oldest name for any member of this complex is *A. apurense*, based on *Bignonia apurense* H. B. K. from the middle Orinoco region of Venezuela. I have previously (Gentry, 1974a) identified the type of *A. apurense*, which lacks fruit,

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with the wing-seeded form of this complex, mainly because of its small subcoriaceous leaflets. However, only specimens with wingless seeds have been subsequently collected along the Orinoco so the *A. apurense* type should presumably be identified instead with one of the two wingless-seeded forms. The leaflets of the type collection are puberulous beneath, as are those of several collections of the form with subglobose capsules and splitting valves. Although this character is not constant [e.g., *Gentry et al. 10694* (MO) has a 4-valved capsule and leaflets completely glabrous beneath], neither of the other two forms ever has leaflets puberulous below. Typical *A. apurense* is thus the small-capsuled, 4-valved form whose fruit has yet to be described. This capsule is subglobose-ellipsoid, rounded apically and basally, not at all compressed, 4-sulcate, splitting into 4 parts at maturity with each valve splitting down the midline, 2.4–6 cm long, each half-valve 1.3–2.5 cm wide, slightly lepidote when young, becoming densely papillate, drying tannish; seeds thick, wingless, 1.2–2 cm in diameter.

In my opinion the difference between the fruit described above for *A. apurense* and that of the other two forms is adequate for specific segregation. The oldest available name for either (presumably) 2-valved form is *A. inundatum*. As long as winged versus wingless seeds are not considered adequate to justify specific segregation (see Gentry, 1973; Sandwith, 1955; Hunt, 1972), both the wing-seeded and wingless-seeded entities may be included in *A. inundatum*. The type of *A. inundatum* may represent the wingless-seeded form since no wing-seeded collections of this complex from Guiana or Amazonia have been seen. *Adenocalymma inundatum* var. *surinamense*, as defined by its wingless seeds, would thus be synonymous with typical *A. inundatum*, and a new infraspecific name for the northern entity with winged seeds would be necessary. Nevertheless, it seems advisable to retain the extant usage—*A. inundatum* var. *surinamense* with wingless seeds, *A. inundatum* var. *inundatum* with winged seeds—until fruiting material from Amazonian Brazil is available.

Adenocalymma purpurascens Rusby, Descr. S. Amer. Pl. 121. 1920.

This species ranges from Bolivia to Venezuela and was treated by Sandwith (in the herbarium) as a synonym of *A. bracetolatum* DC. The fruit of neither *A. purpurascens* nor *A. bracteolatum* has been described. A recent collection [*Gentry et al. 10672* (MO, VEN, duplicates to be distributed) from Bolívar, Venezuela] of flowering and fruiting material of *Adenocalymma purpurascens* taken from the same plant solves a longstanding puzzle and adds additional evidence of the inability of presence or absence of fruit wings to serve as an absolute generic criterion (cf. Gentry, 1973, 1974b, 1974c).

The fruit of this species proves to be an oblong uncompressed capsule with the valves woody and prominently thick-winged along each margin. The fruit is thus tetragonal with raised angles in cross section. It is 10–19 cm long, 2.5–3.5 cm wide (including wings), 3–5 cm thick (including wings), drying light brown, the midrib not visible, glabrous, the surface slightly wrinkled-striate, the wrinkles making an acute angle with the axis of fruit. The seeds are bialate, 1.1–1.8 cm long, 3.3–6 cm wide, the wings more or less hyaline-membranaceous and indistinctly demarcated from the rather thick brown seed body.

This striking fruit is unique in *Adenocalymma* because of its conspicuous *Cuspidaria*-like wings. This prompted the late Dr. Sandwith to tentatively determine a fruiting collection (*Seibert 2012* from Madre de Dios, Peru) as *Cuspidaria* sp. nov. despite the collector's field notes that the plant was the same species as his number *2011*, the latter an obvious *Adenocalymma* in flower. The identity of this interesting collection had otherwise remained an unsolved mystery.

Actually, Seibert's flowering collection is not *A. purpurascens* but *A. impressum* (Rusby) Sandw. It is no wonder that the collector confused the two species: *A. purpurascens* and *A. impressum* are twins vegetatively. The main vegetative difference between the two species is a quantitative one—the pale-drying veins and veinlets of *A. purpurascens* dry a lighter color than those of *A. impressum*. In flower the smaller (6–9 by 5–7 mm) calyx with an irregularly toothed margin of *A. purpurascens* is quite distinct from the larger (11–14 by 7–12 mm) campanulate calyx with a truncate margin (remotely and minutely 5-denticulate) of *A. impressum*. The bracts and bracteoles of the latter species also tend to be slightly larger. In fruit these two plants are utterly distinctive, the subterete linear-oblong capsule of *A. impressum* showing no resemblance to the winged capsule of *A. bracteolatum*.

Discovery of the winged fruit of *A. purpurascens* also creates a problem. The type of *A. bracteolatum* (*d'Orbigny 758*, P) from Mato Grosso lacks the 4-ridged tetragonal ovary otherwise associated with the wing-fruited species. Perhaps *A. purpurascens* is not the same as *A. bracetolatum* after all? This suspicion is confirmed by two Mato Grosso collections at BM identified as *A. croceum* S. Moore. The flowering type of *A. croceum* proves to be the second collection of *A. bracteolatum* (Gentry, 1976), likewise lacking a tetragonal ovary. The second collection of *A. croceum* is in fruit, comes from the same area as both of the flowering collections, and agrees vegetatively with them. It is clearly *A. bracteolatum*. The fruit of *A. bracteolatum* is oblong and subterete with completely unwinged woody valves. *Adenocalymma purpurascens* with its strikingly winged fruits must be distinct from *A. bracteolatum*. The only apparent characters, besides the ovary, for separating flowering *A. bracteolatum* from *A. purpurascens* are the tenuous ones of dark brown-drying (rather than black) inflorescence branches and a very slightly larger calyx. I cannot distinguish sterile material of these two species. The small leaves cited by Bureau & Schumann (1896–1897) as characteristic of *A. bracteolatum* are present only in the inflorescence; even some sheets of the type collection include the larger leaves characteristic of both it and *A. purpurascens*.

Amphilophium paniculatum (L.) H.B.K. in Venezuela.

Three forms of this variable species, each characterized by its fruit, occur in Venezuela. The flowers of the three are indistinguishable. One of these forms occurs in the Sierra de Imataca region of Delta Amacuro and adjacent Bolívar State. These plants have very large (10–12 cm long, 4–5 cm wide, 1–3 cm thick), relatively flat capsules with muricate-rugose surfaces having the conspicuous projections widely scattered. Vegetatively these plants are distinguished by the yellowish, very finely and densely dendroid tomentose lower leaf surface. The

second form has a smooth granular-textured fruit surface, without prominent ridges or projections. This form has the leaves densely lepidote but otherwise glabrous beneath, except for tufts of long flexuous, mostly simple trichomes in the nerve axils and minute subappressed simple trichomes along the main nerves. It occurs along the dry inner base of the Cordillera de la Costa with fruiting collections from Anzoategui, Miranda, Guárico, and Portuguesa States. This is the fruit type which occurs throughout the range of the species outside Venezuela. The third fruit form is similar to the preceding in size and convex valves, but the valves are sharply and closely reticulate-wrinkled, the wrinkles almost muricate. The leaflets associated with these fruits vary from quite densely dendroid pubescent beneath, especially along the main veins (*Gentry et al. 11172*), to densely lepidote but otherwise essentially glabrous (*Agostini 110*). Most trichomes of these plants are dendroid and stiff; tufts of lax simple trichomes in the nerve axils beneath are uniformly absent. These collections come from Portuguesa, Barinas, and Lara States and the Distrito Federal; I have also seen a collection [*Davidse 5219* (COL, MO)] from Vichada Territory in the Colombian Llanos. A fourth form of *A. paniculatum*, characterized by large leaflets having a denser, uniformly dendroid, rather coarse indumentum, is also found in Venezuela; this has been called *A. macrophyllum* H.B.K. Its fruits are unknown.

Outside Venezuela only the smooth surfaced fruit is known, and it is found associated with plants running the whole gamut from lepidote to densely dendroid pubescent leaves. I have previously followed Seibert (1940a) in treating the conspicuously pubescent-leaved forms (including *A. macrophyllum*) as *A. paniculatum* var. *molle* and the less pubescent forms as *A. paniculatum* var. *paniculatum*.

In the absence of fruits, Pittier described two new species of *Amphilophium* from Venezuela based on differences in pubescence. *A. xerophilum* vegetatively matches the smooth-fruited Venezuelan collections and must be considered part of typical *A. paniculatum*. *A. mollicomum* is almost certainly a pubescent extreme (cf. *Gentry et al. 11172, 11179*) of the form with closely reticulate-ridged fruits which probably merits some kind of taxonomic recognition. I propose to treat it as a variety of *A. paniculatum*, **A. paniculatum** var. **mollicomum** (Pittier) A. Gentry, comb. et stat. nov. (based on *A. mollicomum* Pittier, J. Wash. Acad. Sci. 18: 120. 1928.). Although var. *paniculatum* in Venezuela (and adjacent Colombia) can usually be vegetatively separated from var. *mollicomum* by the uniform leaf indumentum described above, the latter's great variation in leaf indumentum is exceeded by extra-Venezuelan smooth-fruited material, and determination of flowering collections is doubtful. In general, collections from the Cordillera de la Costa region are *mollicomum*, while collections outside this area are not. However, the occurrence of *mollicomum*-like pubescent forms outside this area (including the fruiting Colombian collection of bona fide *mollicomum*) and occasional collections with tufted simple trichomes (*Pittier 11566*) inside it indicates some range overlap and/or breakdown of the vegetative characters. The fruits of *macrophyllum* are unknown and its possible identification with var. *mollicomum* remains moot. Only fruiting collections or specimens associated both geographically and by pubescence type with fruiting collections are assigned to

var. *mollicomum* in the *Flora de Venezuela*. The uniformly densely pubescent-leaved forms usually referred to *A. macrophyllum* H.B.K. are still assumed to be *A. paniculatum* var. *molle* in the absence of fruiting material which could prove them to be var. *mollicomum* instead.

Amphilophium paniculatum var. **imatacense** A. Gentry, var. nov.

Distinguitur indumento foliolorum subtili, dense, trichomatibus dendroideis; fructu magno, complanato, dissite muricato-rugoso.

TYPE: VENEZUELA. BOLÍVAR-DELTA AMACURO BORDER: 61°44′W 8°4′N, primary forest near Río Grande o Toro, E of Upata, 300 m, liana, stem dull gray-brownish-green, tendrils gray-brownish-green, leaves papery, slightly glossy dark green above, dull, rough and paler green beneath, immature fruits dull pale green, 15 × 4.5 cm, 8 Apr. 1967, *de Bruijn 1662* (MO, holotype; isotypes WAG (3)).

In contrast to *A. paniculatum* and *A. paniculatum* var. *mollicomum*, the Sierra Imataca plant is vegetatively distinct and homogeneous. It clearly warrants taxonomic recognition. No collections of *A. paniculatum* from this area are known and it may well prove more than a variety. However, the variability inherent throughout this complex makes it prudent to accord it only varietal recognition at present.

Additional collections examined: VENEZUELA. BOLÍVAR: El Palmar hacia Río Grande, Sierra de Imataca, 300 m, bejuco grande, hojas bifolioladas, discoloras, calices verdes, sepalos abiertos, simulando un caliculo, corolla en boton amarilla con apice morado, cuando abierta (bilabiada) purpurea, luego blanca, frutos verrucosos, hasta 15 cm largos, pedasos, especie frecuente, 21 Feb. 1959, *Bernardi 7192* (VEN, F). Tumeremo to Anacoco, N side of Cuyuni River, 19 km from Guyana frontier, 140–200 m, 18 Mar. 1974, *Gentry et al. 10711* (MO, VEN). Sierra Imataca, rainforest between junction with Río Reforma and 1 km below junction along river, between Río la Reforma and Puerto Rico, N of El Palmar, 200–250 m, vine, leaves subcoriaceous, dull green above, gray green below, calyx spreading, gray green, corolla creamy white, *Steyermark 88117* (VEN). DELTA AMACURO: Near the border (Río Grande o Toro) with Estado Bolívar, ca. 61°44′W 8°4′N, low primary forest, liana 20 m high, 5 cm in diameter, leaves papery dull, medium green above, paler beneath, fruits pale green, dull, *Breteler 3833* (VEN, WAG). Bosque pluvial Este de Río Grande, 37 km ENE de El Palmar, high-climbing liana, leaves tawny below, dull green above, corolla deep yellow, 10 Feb. 1964, *Steyermark 93128* (VEN).

Arrabidaea prancei A. Gentry, sp. nov.—FIG. 1A.

Frutex scandens; ramuli subteretes, consociebus glandularum in nodis inter petioles; folia bifoliolata, interdum cirrhis simplicibus, foliolis ellipticis, acuminatis; inflorescentia floribus in paniculis parvis axillaribus dispositis; calyx cupulatus, truncatus, minute 5-denticulatus, lepidotus; corolla alba lavandula suffusa, campanulata supra basem longam tubularem; stamina subexserta, thecis divaricatis; ovarium anguste oblongum, lepidotum; capsula linearis, aliquantum lepidota; semina bialata, brunneola.

Liana; branchlets terete, striate, minutely lepidote or glabrous, when older drying reddish brown with numerous small, slightly raised almost circular lenticels, with 4 phloem arms in cross section; nodes with interpetiolar glandular fields; pseudostipules not evident. Leaves 2-foliolate, often with a simple tendril; leaflets elliptic, acuminate, truncate to broadly cuneate at base, subcoriaceous, 5–15 cm long, 4.2–9 cm wide, minutely lepidote, otherwise glabrous, more or less

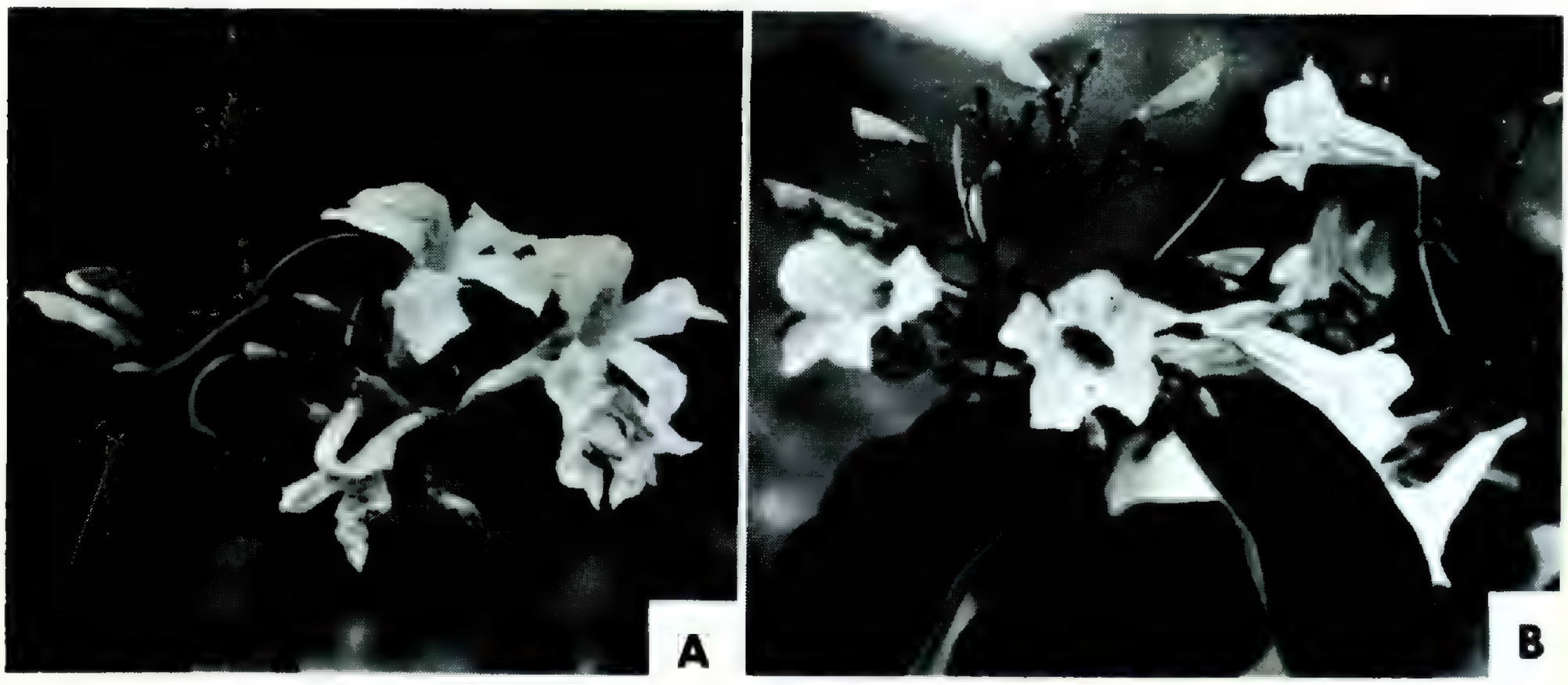


FIGURE 1. A. *Arrabidaea prancei* A. Gentry; photo of type, *Gentry 12882*; × 7/16.—B. *Cuspidaria subincana* A. Gentry; photo of type, *Gentry 12825*; × ½.

conspicuously 3-veined from base, with 3–4 secondary veins on each side; petiolules 0.6–4.5 cm long; petiole 1–4 cm long, lepidote. Inflorescence a few-branched panicle, flattened and wider at and below each joint, lepidote throughout, puberulous only at the joints and on margins of the minute (less than 1 mm long) bracts and bracteoles, the buds elongate, conical, tapering to an almost acuminate point. Flowers with calyx cupular, 7–10 mm long, 3–4 mm wide, more or less truncate, minutely and evenly 5-denticulate, occasionally slightly split on one side, densely lepidote, puberulous on margin and very sparsely in upper half, with often inconspicuous plate-shaped glands in upper half; corolla white or greenish white with the tube tinted purple outside, tubular-infundibuliform above a very long tubular base, 4.5–6 cm long, the tube 3.5–4.5 cm long, 0.8–1.0 cm wide at top, the basal portion 2.0–2.6 cm long, 1.5–2 mm wide, the lobes 1–1.5 cm long, densely puberulous outside and on lobes inside, the upper part of tube glabrous inside, sparsely puberulous at and below level of stamen insertion, becoming densely glandular pubescent between 9 and 15 mm above base of tube and abruptly glabrous below this area; stamens didynamous, subexserted, the anther thecae divaricate, glabrous, each 3 mm long, the longer filaments 1.6–1.8 cm long, the shorter filaments 1.2–1.5 cm long, the staminode 4–5 mm long, insertion 2.2–2.6 cm above base of corolla tube; pistil 4–4.5 cm long, the ovary linear oblong, tetragonal, the 4 angles raised (almost cross-shaped in cross section), 4 mm long, 1 mm wide, very densely lepidote, the ovules rather large, 2-seriate in each locule; disc 0.5 mm long, 1.25 mm wide. Capsule linear, compressed, blunt at apex and base, 25–36 cm long, 1.6–1.9 cm wide, the midline barely or not at all evident, the margins rounded, somewhat lepidote, drying brownish; seeds thin, bialate, the wings completely brown or with a thin hyaline marginal fringe, indistinctly demarcated from body of seed, 1.3–1.6 cm long, 2.6–4.8 cm wide.

TYPE: BRAZIL. AMAZONAS: Km 67 E of Manaus on Manaus-Itacoatiara Road, liana, flowers white, tube faintly lavender above without and sometimes below or within, fragrant, fruits green, 24 Nov. 1974, *Gentry 12882* (INPA, holotype; isotypes MO and to be distributed).

Additional collections examined: BRAZIL. AMAZONAS: Basin of Rio Negro, road from Camanaus to Uaupes airport, roadside, vine, corolla white, exterior of tube purple, 30 Oct. 1971, *Prance et al. 15863* (MO, NY). Rio Purus, Rio Ituxi, Lago Preto, 2 km N of Labrea, forest on terra firme, liana 10 cm diam. at widest point, calyx green-brown, corolla lavender-white outside but darker adaxially white inside, 26 June 1971, *Prance et al. 13757* (MO, NY). Manaus, estrada Manaus-Itacoatiara, km 55, T. firme, argiloso, trepadeira, frutos maduros, 14 Oct. 1960, *Rodriguez & Coelho 1839* (INPA). Estrada Castanho Tupana, entre o km 50–40; flores de color branca, tube violaceo, frutos verdes, 18 July 1972, *Silva et al. 847* (INPA, MO). ACRE: Cruzeiro do Sul, Rio Jurua & Rio Moa, Estrada Alemanha, disturbed secondary forest by road, corolla greenish white tinted purple on exterior, 14 Apr. 1971, *Prance et al. 11834* (NY). PARA: Rio Jari, Monte Dourado, flor lila clara, *Oliveira 4479* (IAN). Rio Jari, Monte Dourado to Munguba, 13 May 1969, *Silva 1955* (IAN). Rio Jari, Planalto A, flor branco aroxeado, 23 Apr. 1969, *Silva 1955* (IAN). Rio Jari, Estrada de Munguba, km 4, 19 Apr. 1969, *Silva 1876* (IAN). Rio Jari, Estrada entre Monte Dourado e Planalto A, km 3, 22 May 1969, *Silva 2030* (IAN).

The affinity of this distinctive new species with *Arrabidaea* is not immediately obvious because of its elongate white corolla. In such features as its racemose-paniculate inflorescence, subexserted anthers, and elongate tubular white flowers it is reminiscent of *Leucocalanthe*. Nevertheless, it shares most of the important characters of *Arrabidaea*, including interpetiolar glandular fields, simple tendrils, stems with 4 phloem arms in cross section, corolla pubescent without, straight divaricate anther thecae, and a conspicuous nectariferous disc. In fact, were one to predict the characteristics to be expected in a species of *Arrabidaea* adapted for hawkmoth pollination, one would come close to a description of *A. prancei*. Its closest relative seems to be *A. triplinervia* which has very similar trinerved leaflets, reduced, almost racemose inflorescences, a similar corolla shape (except for the long narrow basal constriction), and sometimes white flowers.

Cuspidaria subincana A. Gentry, sp. nov.—FIG. 1B.

Frutex scandens; ramuli subteretes, consociebus glandularum in nodis inter petioles; folia trifoliata vel bifoliata, interdum cirrhis simplicibus, foliolis ellipticis, obtusis vel breviter cuspidatis, subtus canescentibus; inflorescentia floribus in panicula dispositis; calyx cupulatus, truncatus, minute 5-denticulatus, puberulus; corolla rubra, tubulo-infundibuliformis; antherarum lobi semicirculares, connectivo crasso; ovarium ovoideum, minute lepidotum; capsula linearis, subteres, puberula, bisulcata, seminibus bialatis.

Liana; branchlets terete, minutely striate, puberulous; interpetiolar glandular fields present; pseudostipules not noticeable; conspicuously lenticellate when older. Leaves 3-foliolate or 2-foliolate with a tendril or tendril scar; leaflets elliptic or obovate-elliptic to subrotund, the apex rounded or abruptly cuspidate, the base rounded to broadly cuneate, 3.5–14 cm long, 2.2–9 cm wide, chartaceous to subcoriaceous, the main veins slightly raised beneath, densely canescent below except the darker-drying veins, glabrous above except on midvein, drying dark brown above, whitish below with the less pubescent main veins contrastingly darker; petiolules 1–3 cm long; petioles 2–5 cm long, puberulous. Inflorescence an axillary or terminal panicle, its branches puberulous. Flowers with the calyx cupular, 5-denticulate, 4–5 mm long, 2–3 mm wide, conspicuously puberulous, eglandular or with a few glands near margin, the marginal teeth often extending as raised lines on upper third of calyx; corolla magenta with a white throat, tubular-infundibuliform, 2.7–4 cm long, 0.7–1.3 cm wide at mouth of tube, the tube 2.3–

3.4 cm long, the lobes 0.5–0.8 cm long, puberulous outside and on lobes and at level of stamen insertion inside; stamens didynamous, the anther thecae bent and reflexed sharply forward near middle, 1–2 mm long, glabrous, the connective extremely thick, extended; pistil 1.7–2.4 cm long, the ovary ovoid, 1.5–1.8 mm long, 1–1.2 mm wide, with two longitudinal furrows on each side, densely minutely lepidote, sometimes also scattered puberulous, the ovules 4-seriate in each locule; disc cupular-pulvinate, 1 mm long, 1.5 mm wide. Capsule linear, terete, 29 cm long, 1.3 cm wide, puberulous, drying grayish, with scattered small lenticel-like glands, each valve with a conspicuous median longitudinal furrow 2–3 mm wide and bordered by a slightly raised line on either side; seeds thin, flattened, bialate, 8–9 mm long, 3.7–4.6 cm wide, the hyaline membranaceous wings sharply demarcated from the seed body.

TYPE: BRAZIL. AMAZONAS: 2–5 km N of Manaus-Itacoatiara Road at km 79 near Rio Preto da Eva, 100–200 m, liana, flowers magenta with white throat, 24 Nov. 1974, *Gentry 12825* (INPA, holotype; isotypes MO, MG, RB, to be distributed).

Additional collections examined: VENEZUELA. BOLÍVAR: Bosques a lo largo de la frontera Venezolano-Brasilera, NE de la Serrania Pia-soi (Pia-shauhy, pia-Savi), 3°53′, 62°46′, 650–800 m, high-climbing vine, leaves subcoriaceous, deep green above, gray-green below, calyx brownish, corolla deep rose, style pink-maroon at tip, whitish below, rachis of inflorescence tawny-green, 5–6 Jan. 1962, *Steyermark 90694* (VEN). BRAZIL. AMAZONAS: 2–5 km N of Manaus-Itacoatiara Road at km 79 near Rio Preto da Eva, 100–200 m, *Gentry 12850* (INPA, MO). Manaus-Caracarai Road (BR 174), ca. km 100, roadside, vine, flowers magenta with white throat, 30 Nov. 1974, *Gentry & Ramos 12924* (INPA, MO). Estrado do Aleixo near Manaus, km 6–7 past INPA, second growth and forest edge, vine, fruits gray green, 2 Dec. 1974, *Gentry 13042* (INPA, MO). Munic. Humayta, near Livramento, Rio Livramento, 12 Oct.–6 Nov. 1934, *Krukoff 6878* (K, MO, NY). Munic. Manaus, road to Aleixo, 12 Aug.–1 Sep. 1936, *Krukoff 8012* (K, MO, NY). Km 55–60 da Rodov. Manaus-Itacoatiara, cipo, sobre chao, flores lilas, 24 Oct. 1963, *Oliveira 2770* (IAN, MO). Vic. of Labrea airport, Rio Purus, Rio Ituxi, fruit green, glaucous, 29 June 1971, *Prance et al. 13974* (MO, INPA, NY). Mata da terra firme, solo argiloso, entre o rio Castanho e o Araca, trepadeira com flores violaceae, 12 July 1972, *Silva et al. 549* (INPA, MO). 7 km N of Manaus on Estrada do Aleixo, vine, flowers light magenta, 21 Nov. 1974, *Gentry & Prance 12787* (INPA, MO). Ca. km 80, Manaus-Caracarai Road (BR 174), road cut, vine, flowers magenta, 30 Nov. 1974, *Gentry & Ramos 12927* (INPA, MO). Ca. km 70, Manaus-Caracarai Road (BR 174), road cut, vine, flowers magenta with white throat, reddish lines above each row of anthers, 1 Dec. 1974, *Gentry 13006* (INPA, MO). Estrada do Aleixo, Manaus, 15 Oct. 1947, *Guedes 24* (IAN).

Haplolophium rodriguesii A. Gentry, sp. nov.—FIG. 2.

Frutex scandens; ramuli sexanguli sine consociebus glandularum in nodis inter petioles; folia bifoliolata, interdum cirrhis fissis, foliolis ellipticis, coriaceis, subtus puberulis; inflorescentia floribus in racemis axillaribus dispositis; calyx cupulatus, margine crispato, stellato-piloso; corolla rubra, tubulo-campanulata, ad medium flexa; stamina didynama, thecis divaricatis; ovarium ovoideum, dense tomentosum; discus patelliformis; capsula ignota.

Liana; branchlets 6-sided, the angles ribbed, drying blackish, puberulous; interpetiolar glandular fields absent; pseudostipules not noticeable. Leaves 2-foliolate with a trifid tendril; leaflets elliptic, abruptly short-acuminate, the base rounded, 15–17 cm long, 9–12 cm wide, coriaceous, the veins and veinlets plane above, raised and intricately and conspicuously reticulate below, immersed-lepidote above, otherwise glabrous, simple-puberulous below, drying olive gray;

FIGURE 2. *Haplolophium rodriguesii* A. Gentry; × ½. [After *Rodrigues 12951* (INPA).]

petiolules 2–4 cm long; petiole 6.5–7.5 cm long, puberulous. Inflorescence a fascicle of axillary racemes, puberulous with stellate trichomes, the flowers borne in pairs along rachis separated by 2–4 cm, each pair of pedicels subtended by two linear bracts 5–7 mm long and 1 mm wide, the pedicels 0.5–1 cm long, with a pair of linear 2–5 mm long bracteoles near middle. Flowers with the calyx having a cupular base and an expanded frilly margin, the base 6–8 mm long and 4–6 mm wide, the frilly margin ca. 5 mm wide, stellate-tomentose, with paired sublinear glandular fields at top of base below the margin; corolla red, aromatic, relatively thick, tubular-campanulate, bent at 90° angle above base, 4–5 cm long, 0.8–1.2 cm wide, the tube ca. 1 cm to the bend, 2–2.5 cm above the bend, the lobes ca. 1 cm long, the throat with two longitudinal ridges, densely pubescent outside, pubescent inside on lobes and at level of stamen insertion, otherwise lepidote inside; stamens didynamous, inserted 7–8 mm from base of corolla tube,

the anther thecae divaricate, 3–4 mm long, the pollen grains 8-colpate; pistil 3.3–3.5 cm long, the stigma elliptic, acuminate, 3–4 mm by 1.5 mm, the style stellate tomentose, the ovary ovoid, 2 mm long, 2 mm wide, densely tomentose, the ovules ca. 8-seriate in each locule; disc patelliform, 1–1.5 mm long, 4–5 mm wide. Capsule unknown.

TYPE: BRAZIL. AMAZONAS: Manaus, estrada do Igarape do Passarinho, terreno firme argiloso, mata, trepadeira com gavinhas, flores roxas, aromaticas, 22 May 1962, *Rodrigues & Chagas 4460* (INPA, holtotype; MO, NY, isotypes).

This remarkable plant, only the second known species of *Haplolophium*, is very distinct from *H. bracteatum* Cham. in its much larger leaves with intricately reticulate and densely puberulous lower surfaces, in its much more open inflorescence, and especially in its very inconspicuous linear inflorescence bracts and bracteoles. Nevertheless, it shares the fundamental characters of the genus including 6-angled branchlets, trifid non-disc-tipped tendrils, 8-colpate pollen, and, most notably, a calyx with a cupular truncate base and a frilly expanded margin. *Haplolophium* is intermediate between *Pithecoctenium* and *Amphilophium*, agreeing with the former in its tubular bent corollas, simple calyx, and echinate fruit and with the latter in its pollen, trifid tendrils, dendroid trichomes, and the presence of a frilly calyx margin. The intricately reticulate and raised venation beneath of *H. rodriguesii* is strikingly like that of *Distictella monophylla* Sandw.

Memora aspericarpa A. Gentry, sp. nov.—FIG. 3.

Arbor parva vel frutex; ramuli subteretes, sine consociebus glandularum in nodis inter petioles; pseudostipulae crassae foliaceae; folia saepe 15-foliolata pinnis principalibus tribus, foliolis lanceolatis vel anguste ellipticis, acuminatis, basi cuneatis vel rotundatis, glabris; inflorescentiae racemosae terminales, bracteis mature deciduis, probabiliter minutis, bracteolis minutis; calyx coriaceous, campanulatus, bilabiatus, extus plerumque glaber intus lepidotus; corolla flava, tubulo-infundibuliformis, extus glabra; stamina thecis divaricatis; pistillum ovario glabre; discus pulvinatus; fructus oblongus, teres, exasperatus, seminibus exalatis, maxime crassis.

Small tree or shrub, rarely subscandent, to 3 m tall; branchlets subterete, glabrous, lenticellate; nodes without interpetiolar glandular fields; pseudostipules thick-foliaceous, obovate, rounded. Leaves 2–3-compound, usually 15-foliolate with three 5-foliolate primary pinnae, each leaflet of lowermost leaflet pair of the terminal pinna sometimes replaced by a 3-foliolate secondary division, the leaf thus to 19-foliolate; tendrils not seen; leaflets lanceolate to narrowly elliptic, less commonly elliptic or narrowly ovate, acuminate, cuneate to rounded at base, subcoriaceous, 4–17 cm long, 1.2–8 cm wide, completely glabrous or with a few inconspicuous simple trichomes along midvein above; petiolules and petiole very sparsely puberulous or glabrate. Inflorescence a contracted terminal raceme, drying dark, the pedicels 0.8–1.5 cm long, inconspicuously short-puberulous, the bracts early deciduous, probably minute, the bracteoles minute, subulate, 1–4 mm long, ca. 1 mm wide, attached at or below middle of pedicel 5–10 mm below calyx, lepidote inside, finely pubescent at tip and along margin. Flowers with the calyx coriaceous, campanulate, bilabiately split ⅓–½ its length, 10–12 mm long, 8–10 mm wide, somewhat lepidote, with a few trichomes at apices of lobes,

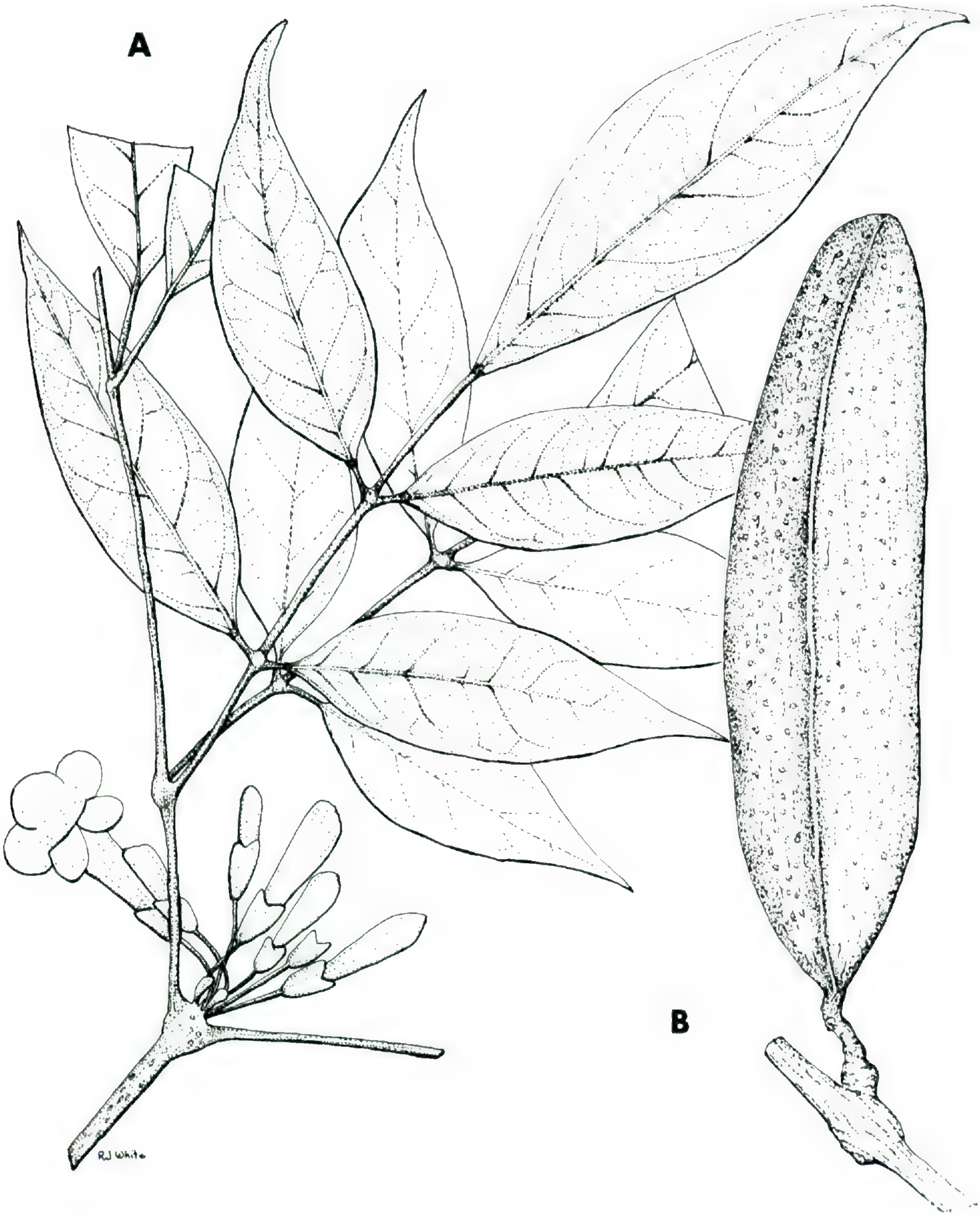


FIGURE 3. *Memora aspericarpa* A. Gentry.—A. Habit; × ½. [After *Steyermark 105375* (VEN).]—B. Fruit; × ½. [After *Aristeguieta & Pannier 1842* (VEN).]

otherwise glabrous outside, glandular lepidote inside, eglandular outside; corolla yellow, tubular-infundibuliform, 5.5–7.5 cm long, 1.2–2.4 cm wide at mouth of tube, the tube 4–5.8 cm long, lobes 1–1.5 cm long, mostly glabrous, the lobes sometimes with a few marginal trichomes, villous at and below level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3–4 mm long, the longer filaments 3.7–3.8 cm long, the shorter filaments 2.7–2.8 cm long, the stami-

node 10–11 mm long, insertion 16–18 mm from base of corolla tube; pistil 4.8–5 cm long, the ovary linear-oblong, 3 mm long, 1 mm wide, glabrous; disc patelliform, 1–1.5 mm long, 2.5–3 mm wide. Capsule oblong, terete, 8–22 cm long, 3.3–4.7 cm in diameter, the apex obtuse or acutish, the base more or less rounded, macroscopically conspicuously rough-surfaced with many minute rather flat tubercles somewhat resembling coarse sandpaper in appearance, these tubercles coalescing and not individually distinct under a lens; seeds very thick, wingless, angulate, 2.3–2.5 cm long, 2.0–3 cm wide, the hilum broad, convex, 7–12 mm wide, 17–21 mm long.

TYPE: VENEZUELA. YARACUY: Selva nublada sobre piedras calcareas, entre el pueblo de Aroa y Altamira, 1050 m, small tree 3 m tall with slender trunk 1 cm diam., divergently branched above, corolla yellow, 22 Jan. 1972, *Steyermark 105375* (MO, holotype; VEN, isotype).

Additional collections examined: VENEZUELA. DISTRITO FEDERAL: Caruao, (fruit), *Pittier s.n.* (VEN). YARACUY: Montana que queda enfrente del caserio de Quebrada Seca, trepadora de olor a ajos, 2 July 1953, (fruit), *Aristeguieta & Pannier 1842* (VEN). TACHIRA: A la orilla de potreros, cerca a Jordan, bosque humedo tropical, arbolito, approx. 3 m alto, 26 Apr. 1964 (fruit), *Yjjaz 351* (MY). LARA: Terepaima, 1300–1600 m, arbusto trepador de flores amarillas (flowers, fruits), 24 Mar. 1959, *Trujillo 4116* (MY).

This species is restricted to upper elevations (mostly over 1,000 m) along the Venezuelan coastal cordillera east to the Distrito Federal.

Memora aspericarpa differs from *M. schomburgkii* (DC.) Miers in its smaller bilabiate (rather than spathaceous) calyx and thick-valved rough-surfaced fruit. It is perhaps most closely related to *M. cladotricha* Sandw. even though that species belongs to a different section of the arbitrarily subdivided genus. It resembles *M. cladotricha* in habit and fruit although lacking foliaceous inflorescence bracts and bracteoles. The fruit of *M. cladotricha*, though similar to that of *M. aspericarpa*, has a macroscopically smoother surface with a less dull texture. The papillae covering the fruit of *M. aspericarpa* tend to coalesce and are individually obscure when seen through a lens; the papillae of *M. cladotricha* are individually distinct microscopically.

Memora tanaeciicarpa A. Gentry, sp. nov.

Frutex scandens; ramuli teretes, glabrati, sine consociebus glandularum in nodis inter petioles; folia 2–3-ternata, interdum cirrhosa, foliolis ellipticis vel ovatis, acuminatis; inflorescentia racemosa, axillaris, bracteis caducis; calyx campanulatus, minute 5-denticulatus; corolla tubulo-infundibuliformis, tubo extus puberulo; stamina thecis divaricatis; ovarium oblongum, puberulum; discus pulvinatus.

Liana; branchlets terete, glabrate, finely striate, elenticellate or with inconspicuous elongate lenticels; nodes without interpetiolar glandular fields or pseudostipules. Leaves 2–3-ternate, the terminal 3 leaflets sometimes replaced by a simple tendril; leaflets elliptic to ovate, acuminate, the base cuneate to truncate, chartaceous, 4–15 cm long, 1.5–7 cm wide, very minutely and inconspicuously scattered lepidote or lepidote-papillose above and below, otherwise glabrous or very sparsely and minutely subpuberulous along midvein below, drying olive with contrasting yellowish or reddish main veins below, the main veins plane

above, prominent below; petiolules and petiole glabrous or subpuberulous adaxially. Inflorescence an axillary raceme, puberulous, the bracts early deciduous, 2–3 mm long, 2–3 mm wide, yellowish puberulous and glandular, bracteoles absent. Flowers with the calyx campanulate, truncate, minutely 5-denticulate, 10–13 mm long, 6–9 mm wide, densely yellow-tomentose with branched trichomes, with scattered black-drying glands in upper half; corolla tubular-infundibuliform, ca. 4 cm long (mature corollas seen all shrivelled and partially destroyed), densely puberulous outside and on lobes inside, with plate-shaped glands at base of lobes outside, the tube mostly glabrous inside, densely villous at and below level of stamen insertion; stamens inserted 12–13 mm above base of corolla tube, the filaments 1.1–2.1 cm long, the anther thecae divaricate, 2.5–3 mm long; pistil 3.2–3.3 cm long, the style puberulous with branched trichomes, the ovary oblong, 3 mm long, 1 mm wide, densely puberulous; disc annular-pulvinate, 1 mm long, 2.5 mm wide.

TYPE: BRAZIL. AMAZONAS: Manaus, km 10 estrada Manaus-Itacoatiara, trepadeira com flores amarelas na mata de t. firme solo argiloso, 16 May 1972, *Loureiro, Pires & Athanagildo s.n.* (INPA 35794) (INPA, holotype; MO, isotype).

Additional collections examined: VENEZUELA. AMAZONAS: Dept. Apures, Río Orinoco, alrededores de Siquita entre la Isla Castillito y San Fernando de Atabapo, 100–140 m, *Bunting et al. 3631* (MY). BRAZIL. AMAZONAS: Ducke Forest Reserve, km 26 on Manaus-Itacoatiara road, sterile vine, tendrils simple, stems rough, greenish, 23 Nov. 1974, *Gentry 12820* (MO, INPA). PARA: Cabeceiras do Rio Uruará, flancos do Planalto Amazonico, municip. de Prainha, cipó ao longo do rio, 11 May 1955, *Fróes 31881, 31886* (both IAN). Santarém, Rio Maicá, Serra de Taperinha, capoeira do pé da serra, cipó robusto, fruto verde, 5 Feb. 1968, *Silva 1371* (MG).

This is quite unlike any other species of *Memora* in its large 4-valved capsule, its puberulous style and ovary, its yellowish-red puberulous 5-denticulate calyx, and its puberulous corolla tube. Except for the 2–3-ternate leaves it seems closer to *Adenocalymma comosum* and allies than to other *Memora* species, additional evidence of the artificiality of the separation of *Memora* and *Adenocalymma*.

Tanaecium apiculatum A. Gentry, sp. nov.—FIG. 4.

Frutex scandens; ramuli teretes, sine consociebus glandularum in nodis inter petioles; folia bifoliolata, foliolis ellipticis, apiculatis, leviter lepidotis aliter glabris; inflorescentia floribus in racemo dispositis; calyx tubulosus, lepidotus, minute puberulous; corolla alba, elongato-tubuloso, puberula; stamina subexserta; ovarium lineare, dense lepidotum; fructus juvenis linearis, lepidotus.

Liana; branchlets terete, striate, hollow, glabrous; interpetiolar glandular fields and pseudostipules absent. Leaves 2-foliolate with a (simple?) tendril; leaflets elliptic, sharply apiculate, rounded at the base, 16–18 cm long, 8.5–9 cm wide, membranaceous, lepidote above, inconspicuously scattered-lepidote below, otherwise glabrous, drying gray with a whitish cartilaginous margin, the apiculation with plate-shaped glands; petiolules 1.5–2.7 cm long; petioles 3.2–3.6 cm long, very slightly lepidote. Inflorescence a raceme, minutely lepidote and densely mealy puberulous, the rachis ca. 20 cm long, the pedicels ca. 0.5 cm long, the bracts triangular, 3–4 mm long, 3 mm wide, glandular, caducous in bud. Flowers with the calyx tubular, very shallowly 5-denticulate, 3.0–3.5 mm long, 6–7 mm

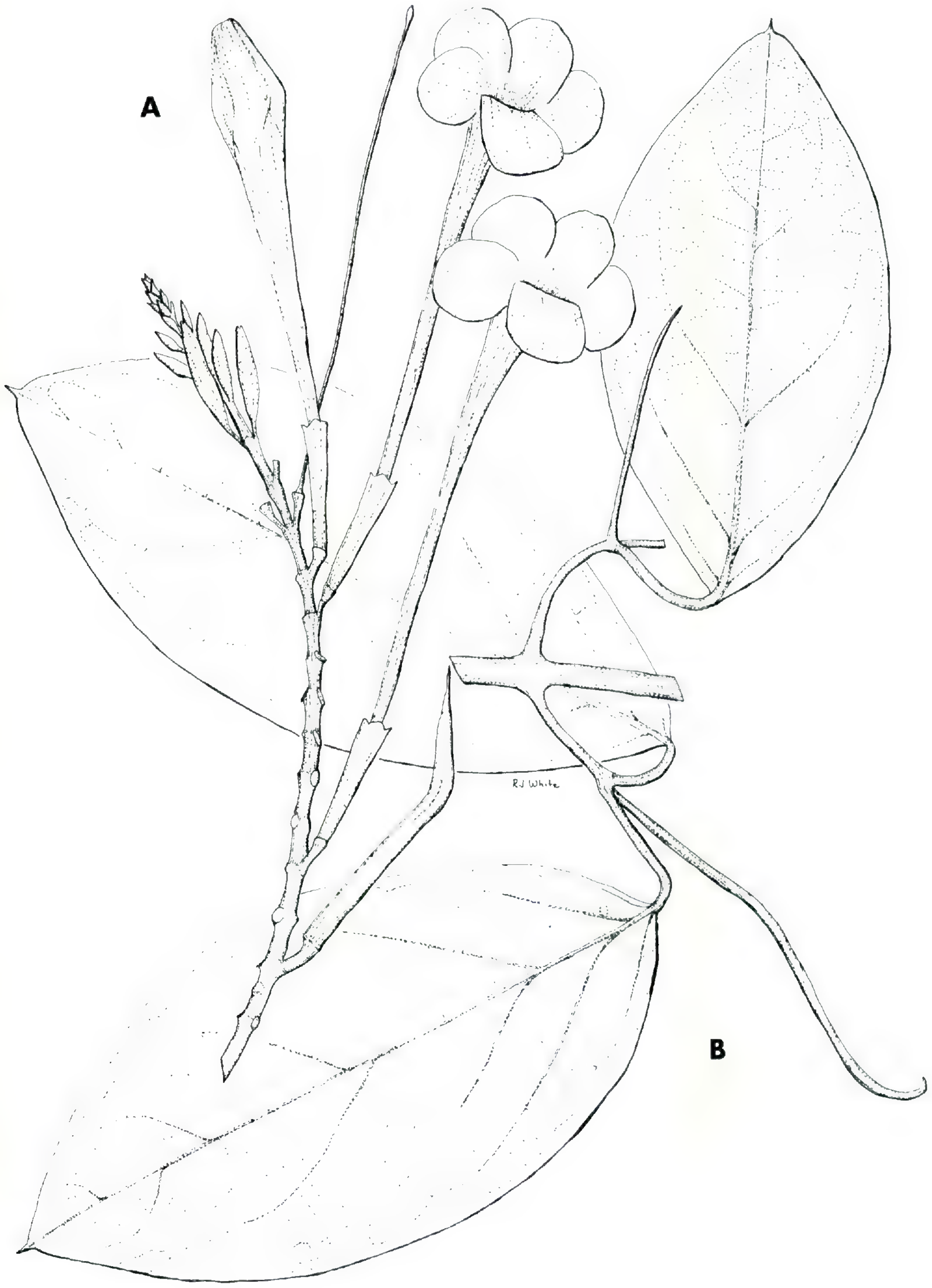


FIGURE 4. *Tanaecium apiculatum* A. Gentry.—A. Inflorescence; × ½.—B. Leaves; × ½. [After *Smith 226* (US).]

wide, lepidote and minutely puberulous with stellate trichomes, circumscissile and falling with corolla; corolla white, elongate-tubular, expanded apically, 15–16 cm long, 14–16 mm wide at the mouth, the tube 13–14 cm long, the lobes 2–2.5 cm long, puberulous outside, the lobes glandular-lepidote inside, the tube glabrous inside except for a few lepidote scales at base of filaments, with linear fields of plate-shaped glands near base of lobes outside; stamens didynamous, the anthers subexserted, the thecae 4(?) mm long, the filaments 10–12 cm long, insertion 9 cm above base of corolla tube, staminode 1 mm long, inserted 8.3 cm above base of tube; pistil 14–16 cm long, the ovary linear, the base somewhat widened, densely lepidote, 4–6 mm long, ca. 1 mm wide; disc annular-pulvinate, ca. 1 mm long, ca. 3 mm wide. Very young fruit linear, subterete, 8 cm long, 0.6 cm wide, scattered lepidote and with a few platter-shaped glands.

TYPE: VENEZUELA. MONAGAS: Caicara, important vine of the heavy woods, flowers white, wet woods, "caratero," 15 May 1952, *Smith 226* (US 2121468, holotype; US 2121469, isotype, MO fragments).

This plant is utterly distinct from any other species of Bignoniaceae. Its elongate tubular white flowers are those characteristic of *Tanaecium* but the long tubular circumscissile calyx is unique in that genus. Cartilaginous leaflet margins are also unique in *Tanaecium* although found in several species of *Adenocalymma*; the striking terminal apiculations of the leaflets of this species are found in no other species of Bignoniaceae.

Tynnanthus villosus A. Gentry, sp. nov.—FIG. 5.

Frutex scandens, in omnes partes villosus, sine consociebus glandularum in nodis inter petioles; pseudostipulae foliaceae; folia bifoliolata, foliolis oblongo-ellipticis; inflorescentia floribus in panicula axillari dispositis; calyx cupulatus, subtruncatus, puberulus; corolla cremea, bilabiata, extus puberula; stamina didynama, thecis divaricatis, flexis; ovarium conicum puberulum; discus deficiens; capsula ignota.

Liana; branchlets terete, striate, villous with ca. 1 mm long reddish yellow trichomes; interpetiolar glandular fields absent; pseudostipules foliaceous, 0.9–1.5 cm by 0.8–1.5 cm. Leaves 2-foliolate with a tendril or tendril scar; leaflets more or less oblong-elliptic, acuminate, the base asymmetrically rounded thus usually subcordate on one side, 5–11 cm long, 3–7 cm wide, membranaceous, the main veins raised below, velutinous below with simple trichomes especially along the main veins, less conspicuously pubescent above, drying olive; petiolules 1–1.5 cm long; petioles 2–4 cm long, conspicuously villous. Inflorescence a racemose axillary panicle, villous, the rachis 4–12 cm long, the short, 2–5 mm long peduncles at right angles to it, each bearing 2–3 flowers and subtended by a narrow caducous bract 2–3 mm long. Flowers with the calyx cupular, subtruncate or minutely 5-denticulate, 1.5–2 mm long, ca. 2 mm wide, pubescent, eglandular; corolla cream ("amarillo blancuzco"), bilabiate, ca. 0.5 cm long, split about half its length, the 2 upper lobes almost fused, the 3 lower ones ca. 2 mm long, puberulous outside, inside puberulous on lower 3 lobes, floor of tube, at level of stamen insertion and on margins of upper 2 lobes; stamens didynamous, the anther thecae 1 mm long, divaricate and reflexed forward from a basal twist, the connec-

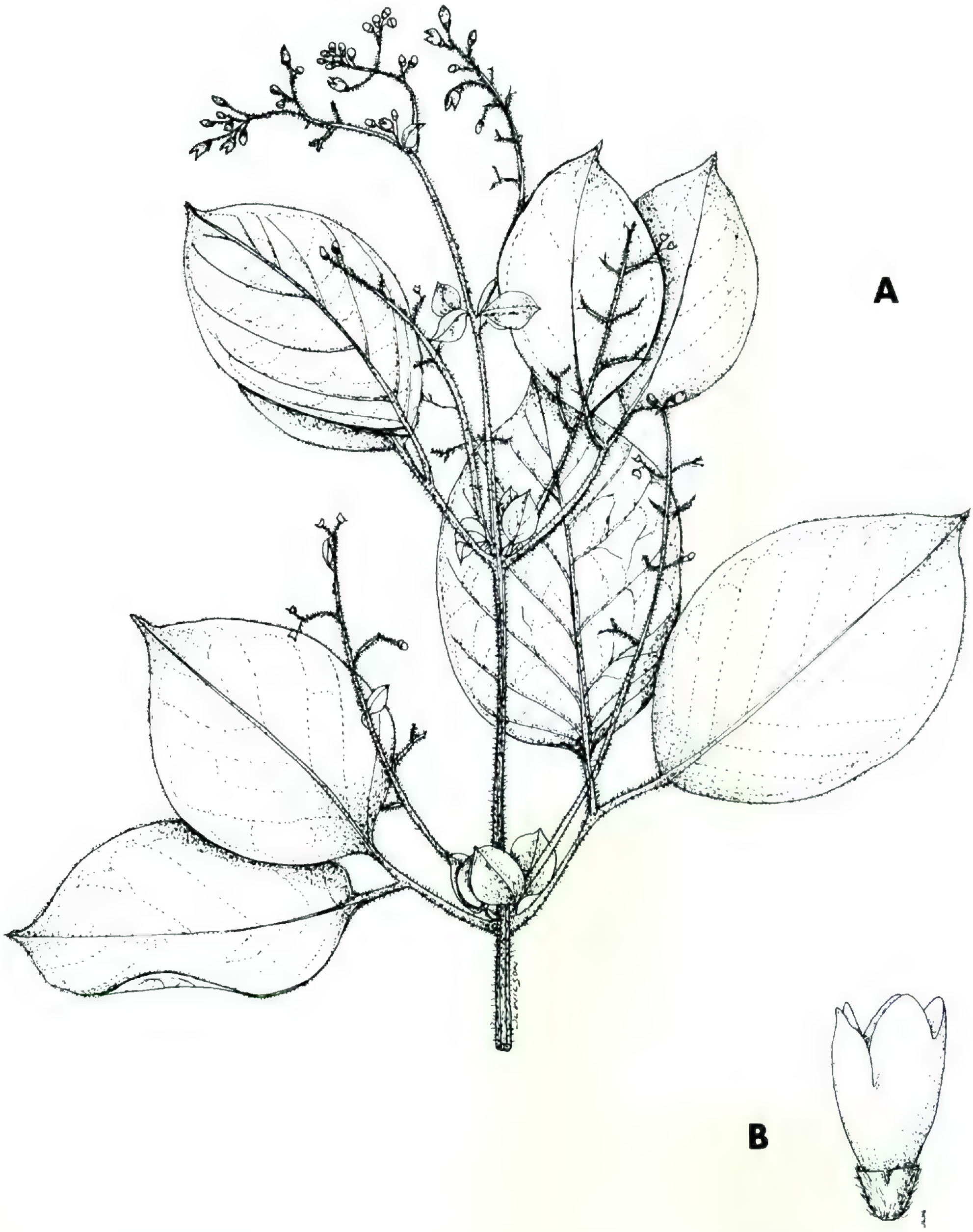


FIGURE 5. *Tynnanthus villosus* A. Gentry.—A. Habit; × ½.—B. Flower; × 5. [After *Schunke* 6852 (MO).]

tive extended 0.2 mm beyond anther attachment, the longer filaments ca. 2 mm long, the shorter filaments ca. 1.5 mm long, the staminode 1 mm long, insertion 0.5 mm from base of corolla tube; pistil 3 mm long, the stigma narrow, bilamellate, the style pubescent toward base, the ovary conical, ca. 1 mm long, 1 mm wide at base, densely pubescent, the ovules 3–4-seriate in each locule at bottom of ovary and 2-seriate at top; disc not apparent. Capsule not known.

TYPE: PERU. SAN MARTÍN: Prov. Mariscal Caceres, Dtto. Tocache Nuevo, Quebrada de Canuto, 400 m, liana de 8–9 m, flores amarillo blancuzco, sepalos brilliant yellow-green, en bosque secundario y con abundante luz solar, 18 Aug. 1973, *José Schunke Vigo* 6852 (MO, holotype; isotypes to be distributed).

Additional collection examined: PERU. HUANUCO: Hills E of Tingo Maria, sterile liana, *Croat 21121* (MO).

This unmistakable plant has no obvious affinities with other species of *Tynnanthus*. It differs markedly from all other species of the genus in its shaggy indumentum, its narrow almost racemose inflorescence, and its persistent foliaceous pseudostipules. Foliaceous pseudostipules are occasionally also found in the very different *Tynnanthus myrianthus* Bur. & K. Schum., but mostly on young branchlets.

Tecoma pedicellata Bur. & K. Schum. in Mart. Fl. Bras. 8(2): 336. 1897.

Handroanthus pedicellatus (Bur. & K. Schum.) Mattos, Loefgrenia 50: 4. 1970.

Bureau and Schumann noted the close relationship of their new species, actually a *Tabebuia*, with *Tabebuia chrysotricha* (Mart. ex DC.) Standl. but considered it distinct on account of its longer pedicels, smaller corolla and calyx, and different calyx indumentum. The species is known only from the type collection, *Glaziou 1476* from Corcovado, Rio de Janeiro, Brazil. Presumably the holotype at Berlin has been destroyed. Isotypes at BR, K, and P have flowering branchlets resembling *Tabebuia ochracea* (Cham.) Standl. detached from branchlets with leaves identical to those of *Tabebuia chrysotricha*. Could the Glaziou gathering be a mixture of these two species? A second isotype at Paris proves the suspicion well founded. This sheet has, in addition to two detached flowering branchlets resembling *Tabebuia ochracea*, a branchlet bearing both leaves and flowers. The attached flowers are those of *Tabebuia chrysotricha*, and *T. pedicellata* is indeed based on a mixed collection. I propose that *Tecoma pedicellata* be rejected under Article 70 of the Code of Nomenclature since the name was based on a type consisting of two or more discordant elements.

ONOHUALCOA & MANSOA

Mansoa verrucifera (Schlecht.) A. Gentry, comb. nov.

Bignonia verrucifera Schlecht., Linnaea 26: 655. 1853. TYPE: Venezuela, Curucati, *Wagener 307* (not seen).
Onohualcoa verrucifera (Schlecht.) A. Gentry, Ann. Missouri Bot. Gard. 60: 885. 1974 (1973). (Includes complete synonymy.)

The monotypic genus *Onohualcoa* has been characterized (Sandwith, 1947) by its trifid tendril, rugose-warty calyx with ribs ending in subulate teeth, pink corolla, and tuberculate-echinate capsule. Dugand (1946) noted the differences between *Onohualcoa* (as *Bayonia*) and *Adenocalymma*, *Pseudocalymma* (now included in *Pachyptera*), *Chodanthus* (now included in *Mansoa*), and *Petastoma* (now included in *Arrabidaea*). He separated his *Bayonia* from *Chodanthus* by the latter's lack of prominent calyx ribs and tubercles on its capsules, although

noting that the fruit is otherwise similar. The other genera mentioned by Dugand are clearly less closely related. Sandwith (1947) emphasized that *Onohualcoa* should be compared with *Mansoa* with a similar inflorescence but a smooth elongate-linear capsule.

I have previously (Gentry, 1974a) accepted Sandwith's interpretation of *Onohualcoa* but united the two species recognized by him. On the other hand, Standley & Williams (1974) inexplicably sink *Onohualcoa* back into utterly unrelated *Adenocalymma*.

Recently I was able to see *Mansoa difficilis* (Cham.) Bur. & K. Schum. in flower in the field and was surprised by its striking resemblance to *Onohualcoa*. A reexamination of the differences separating *Onohualcoa* and *Mansoa* shows that they are very closely related and should be united. In addition to the general similarity between the two genera (see Fig. 6) in such characteristics as subulate calyx teeth, the peculiar inflorescence, tendency to 3-foliolate leaves and 3-veined leaflets, corolla shape, color and pubescence, trifid tendrils, ovules 2-(–4-) seriate in each locule, and large nectariferous disc, may be added two more important similarities.

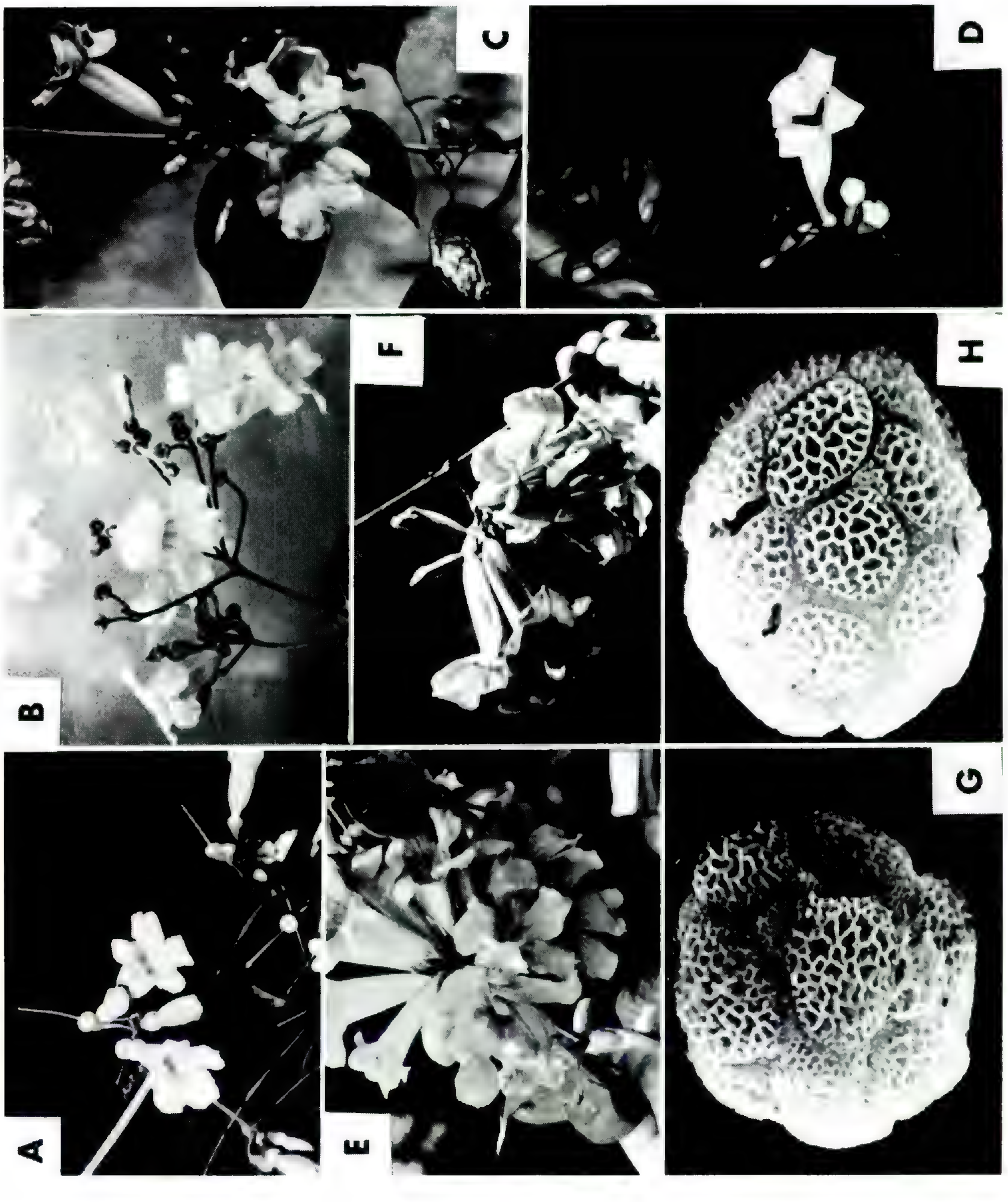
The pollen of *Onohualcoa* has not been described. That of *Mansoa* is of an unusual and very characteristic camporeticulate form with the alveolate exine broken into numerous discrete patches (Fig. 6). The pollen of *O. verrucifera* (Fig. 6) proves to be the same as that of *Mansoa* and strongly supports the union of the two genera (Tombs & Gentry, in preparation).

A second piece of new evidence comes from the capsules of the two genera. *Onohualcoa*'s chief claim to generic rank is its echinate-tuberculate capsule. The known capsules of *Mansoa* are relatively smooth-surfaced, although that of *M. difficilis* usually has raised ridges and may have a beaded almost subtuberculate surface texture. However, fruiting specimens of a new species of *Mansoa* from northeastern Brazil are now at hand which have the same type of echinate-tuberculate surface as *Onohualcoa* (see below). If the fruit of *Onohualcoa* is not unique, then the genus cannot possibly be maintained as distinct. Even were the fruit distinct, merger with *Mansoa* would seem in order—the general trend now emerging in Bignoniaceae (Gentry, 1973, 1974b) is of genera defined by similar floral and vegetative characters with differences in fruits often characterizing only species and varieties.

Mansoa onohualcoides A. Gentry, sp. nov.

Frutex scandens; ramulis teretibus, sine consociebus glandularum in nodis inter petioles; folia trifoliolata vel bifoliolata cum cirrho trifido, foliolis ovatis vel ellipticis, fere glabratis; inflorescentia anguste paniculata, axillaris; calyx cupulatus, 5-setaceus setis 1–2 mm longis, puberulus; corolla tubulo-infundibuliformis, tubo extus glabro; ovarium anguste oblongum, lepidotum vel lepidoto-tuberculatum; discus pulvinatus; capsula anguste oblonga, teres, verrucoso-tuberculata, seminibus bialatis.

Vine; branchlets terete, finely striate, with minute round whitish lenticels; nodes without interpetiolar glandular fields or pseudostipules. Leaves 2–3-foliolate, sometimes with a trifid tendril; leaflets narrowly ovate to elliptic, acute to acuminate, the base rounded to truncate, chartaceous, 2–11 cm long, 1–5 cm wide,


A
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distinctly scattered-lepidote above and below, otherwise glabrous or subpuberulous at base of midvein above and below, with clusters of plate-shaped glands in lower nerve axils below, drying olive to blackish olive, the main veins plane above, prominent below; petiolules 0.3–2.5 cm long; petioles 0.5–3 cm long, puberulous. Inflorescence very narrowly paniculate, the lateral branches each 2–3-flowered, puberulous, ebracteate. Flowers with the calyx cupular, 5–8 mm long (without teeth), 5–6 mm wide, basically truncate, 5-setate, the subulate teeth 1–2 mm long, very briefly extended as ridges near apex of calyx, puberulous; corolla tubular-infundibuliform, 4–4.5 cm long, the tube 3–3.5 cm long, the lobes ca. 1 cm long, the tube mostly glabrous outside, becoming sparsely puberulous toward top, glabrous inside except at level of stamen insertion, the lobes puberulous outside and inside; stamens didynamous, included, inserted 7–8 mm above base of corolla tube, the filaments ca. 2.5 cm long, the anther thecae divaricate, 4 mm long, the connective slightly extended; pistil 3 cm long, the ovary linear-oblong, 2.5–3 mm long, 1 mm wide, slightly narrowed toward base and apex, densely minutely lepidote or lepidote-tuberculate, the ovules 4-seriate in each locule; disc patelliform, 0.5–1 mm long, 1.5–2 mm wide. Capsule linear-oblong, subterete, verrucose-tuberculate, the enations ca. 1 mm long, ca. 15 cm long, 1.4 cm wide; seeds bialate, 0.7–0.9 cm long, 2.5–3.5 cm wide, the wings hyaline-membranaceous, clearly demarcated from rather thick brown seed body.

TYPE: BRAZIL. CEARÁ: Serra de Baturité, Quebradas occidentães perto do sertão de Canindé, 24 Aug. 1908, *Ducke s.n.* (MG1594) (MG, holotype).

Additional collections examined: BRAZIL. CEARÁ: Guaramiranga, Matta, "cipo de cesto," 20 July 1908, *Ducke s.n.* (MG1356) (MG). PERNAMBUCO: Brejo de S. José, planta n. 5, 7 Sep. 1960, *Lima 60-3525* (RB). MARANHÃO: Maracassumé River region, Campo do Casins, *Froes 1857* (MO, NY).

This species is somewhat intermediate between *M. difficilis* (Cham.) Bur. & K. Schum., which ranges through most of eastern Brazil, and *M. verrucifera*, which ranges from Mexico to Guyana and south along the Andes to Acre, Brazil. The verrucose-tuberculate fruit is like that of *M. verrucifera* but narrower and with thinner, nonwoody capsule valves and smaller, more widely separated echinations; the thinness of the valves suggests *M. difficilis*, however. Immature fruits are more densely echinate and exactly like those of *M. verrucifera*. The flowers could easily be confused with either *M. difficilis* or *M. verrucifera* but the abbreviated (or absent) calycine ridges, nonverrucose calyx surface, and almost glabrous corolla tube suggest the former. The nonribbed lenticellate branchlets

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FIGURE 6. *Anemopaegma* and *Mansoa*.—A, D. *Anemopaegma*; B–C. *Pseudopaegma*.—A. *orbiculatum* (Jacq.) DC.; × 5/18.—B. A. *oligoneuron* (Sprague & Sandw.) A. Gentry; × 10/27.—C. A. *longidens* DC.; × 1/3.—D. A. *chrysoleucum* (H.B.K.) Sandw.; × 5/18.— E, G. *Mansoa*; F, H. *Onohualcoa*.—E. *M. difficilis* (Cham.) Bur. & K. Schum.; × 10/27.—F. *M. verrucifera* (Cham.) A. Gentry; × 7/27.—G. Pollen of *M. difficilis*; × 780.—H. Pollen of *M. verrucifera*; × 940. Note the similarity of flower shape in *Anemopaegma* and *Pseudopaegma* (A–D) and *Mansoa* and *Onohualcoa* (E–F), the subtruncate calyx like that of *Anemopaegma* in B, and the camporeticulate pollen of both *Mansoa* and *Onohualcoa* (G–H).

are unlike *M. difficilis*; branchlets of *M. verrucifera* are similar but less noticeably lenticellate. Pinnately veined leaflets with gland fields in the axils of several secondary nerves below are different from either species. *Mansoa onohualcoides* provides the heretofore missing link between *Onohualcoa* (i.e., *M. verrucifera*) and other species of *Mansoa*.

In addition to the cited specimens from northeastern Brazil, a collection from southern Venezuela closely resembles *M. onohualcoides* and may be conspecific. The Venezuela collection [*Lizot 90* from Mavacca, Territorio Amazonas (VEN)] has a shorter more noticeably branched inflorescence, lacks conspicuous lenticels, and has leaflets without glandular fields in the nerve axils below, not notably lepidote, and drying reddish black.

PSEUDOPAEGMA & ANEMOPAEGMA

Urban (1916) proposed *Pseudopaegma* as a segregate from *Anemopaegma* based mainly on the 5–6-colpate pollen of the former versus the ecolpate pollen of the latter. However, Gomes (1955) subsequently described the pollen of *Anemopaegma* (based on *A. pachyphyllum* and *A. hilarianum*, species not examined by Urban) as 5–7-colpate and additional species of that genus also prove to have several-colpate pollen like that of *Pseudopaegma* (Tombs & Gentry, in preparation). Clearly pollen does not support generic segregation.

A second character used by Urban to distinguish *Pseudopaegma* from *Anemopaegma* was the presence of subulate calyx teeth in the former but not the latter. However, Sprague & Sandwith (1932) and Sandwith (1955) later undermined this character by describing additional species of *Pseudopaegma* lacking subulate calyx teeth (cf. Fig. 6). Sandwith (1955) went so far as to note that "the length of subulate calyx teeth is suspect [even] as a specific character." The Venezuelan plant described here further proves this point. It usually has quite distinct calyx teeth 2–3 mm long but these are submarginal and sometimes hardly exceed the calyx margin.

A third character separating *Pseudopaegma* from *Anemopaegma* was proposed by Sandwith (1955) who noted the presence of interpetiolar glandular fields only in the former. Interpetiolar glandular fields are a notoriously variable character, even from node to node on the same plant, and are rarely visible on species of *Pseudopaegma* with puberulous branchlets. Moreover, these glands are not present in the new species which is definitively linked to *Pseudopaegma* by its subulate calyx teeth.

Apparently the fruits of none of the six species attributed to *Pseudopaegma* by Sandwith have been described. The fruits of three *Pseudopaegma* species (*P. oligoneuron*, *P. longidens* and the Venezuelan plant) are now at hand and all prove to have the same very characteristic form as those of *Anemopaegma*. In all other characteristics the two genera are also exactly the same (cf. Fig. 6).

There seems to be no basis for continued segregation of *Pseudopaegma* and I propose that it be reduced to synonymy under *Anemopaegma*. Four new combinations are necessary.

Anemopaegma colombianum (Sandw.) A. Gentry, comb. nov.

Pseudopaegma colombianum Sandw., Kew Bull. 1953: 473. 1954. TYPE: Colombia, Meta, *Cuatrecasas 4605* (COL, K, US).

Anemopaegma insculptum (Sandw.) A. Gentry, comb. nov.

Pseudopaegma insculptum Sandw., Kew Bull. 1954: 608. 1955. TYPE: Colombia, Amazonas, *Garcia-Barriga 14617* (COL, K, US).

Anemopaegma oligoneuron (Sprague & Sandw.) A. Gentry, comb. nov.—FIG. 6.

Pseudopaegma oligoneuron Sprague & Sandw., Kew Bull. 1932: 88. 1932. TYPE: British Guiana, Upper Demerara River, *Jenman 4070* (K).

Anemopaegma mirabile (Sandw.) A. Gentry, comb. nov.

Pseudopaegma mirabile Sandw., Kew Bull. 1953: 474. 1954. TYPE: Brazil, Piauhy, *Gardner 2679* (BM, K).

Anemopaegma alatum A. Gentry, sp. nov.

Frutex scandens, ramulis teretibus, sine consociebus glandularum in nodis inter petioles; folia trifoliolata vel bifoliolata cum cirrho trifido, foliolis ovatis, lepidoto-puncticulatis, leviter puberulis; inflorescentia racemosa, axillaris; calyx campanulatus, 5-dentatus dentibus submarginalibus 2–3 mm longis, puberulus; corolla aurata, tubulo-campanulata, tubo glabro; ovarium ovoideum, basiliter contractum; discus pulvinatus; capsula elliptica, complanata, puberula, seminibus suborbiculatis.

Liana; branchlets terete, finely striate, puberulous, elenticellate; interpetiolar glandular fields absent; pseudostipules minutely foliaceous, deciduous. Leaves 2–3-foliolate, the tendrils trifid; leaflets ovate, acute, rounded to shallowly cordate at base, 5–8.5 cm long, 3–6.5 cm wide, chartaceous, conspicuously lepidote-punctate above and below, puberulous along midvein above and main veins and very sparsely over surface below, the margin sometimes subciliate, drying olive to yellowish olive; petiolules 0.2–1.4 cm long; petioles 2.8–3.8 cm long, densely puberulous. Inflorescence an axillary raceme, the rachis and pedicels puberulous, the pedicels ca. 1 cm long. Flowers with the calyx campanulate, conspicuously 5-toothed ("5-winged" when fresh), the margin basically truncate, the subulate teeth submarginal, 2–3 mm long, extended as calycine ridges, 7–10 mm long (with teeth), 7–8 mm wide, puberulous and lepidote, also with plate-shaped glands below margin; corolla tubular-campanulate above a narrowly tubular basal portion, 5–6 cm long, 1.2–1.8 cm wide at mouth of tube, the tube 4.5–5 cm long, the lobes 0.7–0.9 cm long, the tube glabrous outside, the lobes ciliate, otherwise glabrous, the tube glabrous within except at and below level of stamen insertion, sometimes with plate-shaped glands below lobes outside; stamens didynamous, the thecae divaricate, 3–4 mm long, the longer filaments 1.9–2 cm long, the shorter filaments 1.3–1.5 cm long, the staminode 3 mm long, insertion 20–23 mm from base of corolla tube; pistil 4.3–4.4 cm long, the ovary ovoid, 2–3 mm long, 1.5 mm wide, papillose-lepidote, long-stipitate, the stipe 1 mm long and 0.7 mm wide, the ovules irregularly 4-seriate (appearing 2-seriate in cross section) in each locule; disc cylindric, 1.5 mm long, 2 mm wide. Capsule elliptic, thin-valved, flattened, acute at both ends, 5.5–7 cm long, 3–4 cm wide, the midline not at all raised, puberulous, also with scattered plate-shaped glands, drying tannish, the calyx persistent; seeds thin, suborbicular, the wing surrounding body

of seed, 2–2.6 cm long, 2.8–4 cm wide, outer margin of wing hyaline-membranaceous, this distinctly demarcated from the brownish basal portion which is poorly demarcated from the seed body.

TYPE: VENEZUELA. SUCRE: Distrito Sucre, between La Sabana, Los Altos, and La Silleta, towards Zurita, 600 m, corolla yellow and white, 18 Aug. 1973, *Steyermark et al. 107753* (MO, holotype; VEN, isotype).

Additional collections examined: VENEZUELA. BOLÍVAR: Pequeña meseta del Norte de Serranía Cararubán, SE de Canaima, 6°15′, 62°47′, 300–600 m, trepadora, petalos amarillos, caliz verde, 5-alado, vista también en la sabana, 19 Feb. 1964, *Agostini 386* (NY, VEN). Río Carrao, Alto Caroní, alrededores de Salto Hacho, 6°15′N, 62°51′W, 350 m, Mar. 1954, *Cardona 2868* (US). Río Paragua, Salto de Auraima, 275 m, woody vine, corolla tube yellow, lobes white, common at edge of river in this part, 18 Apr. 1943, *Killip 37544* (NY, US). MONAGAS: Selvas del Río Sabaneta, cerca del pueblo de Quiriquire, trepadora de flores blanco-cremoso, crece al margen de la selva, 9 Aug. 1955, *Lasser & Vareschi 4089* (VEN).

This plant keys to *A. jucundum* in Sandwith's key but is most closely related to *A. longidens* on the basis of its conspicuous rather thick calyx teeth, glabrous corolla tube, and only slightly pubescent leaves. It differs from *A. longidens* in lacking glandular fields at the nodes, having subfoliaceous pseudostipules, leaflets densely punctate-lepidote and puberulous along main veins (and slightly over surface) beneath, slightly shorter calyx teeth (2.5–5 mm long in *A. longidens*), and smaller fruit. In addition its leaves dry olive instead of green and the base of the corolla tube is cylindrical rather than flared out around the ovary as in *A. longidens*. *Anemopaegma alatum* is also close to *A. maguirei* Sandw. of Surinam, the type of which has a shorter (4–6 mm long) calyx similarly pilose pubescent but with a sinuate, scarcely denticulate, margin and lepidote-punctate leaves. That species also differs from *A. alatum* in the corolla tube densely lepidote outside, shorter petiolules (2–4 mm long), and lack of subfoliaceous pseudostipules. Treatment of the Venezuelan plant as conspecific with *A. maguirei* is certainly not possible even though a collection [*Cowan 39224* (NY) from British Guiana, determined as *A. maguirei* by Sandwith] somewhat intermediate between *A. maguirei* and *A. alatum* exists. The Cowan collection has a larger (10 mm by 8–9 mm) calyx than *A. maguirei* with minute but definite submarginal denticulations, and the corolla tube is scattered-lepidote outside. It is unlike both *A. maguirei* and *A. alatum*, especially in having its leaflets only very slightly (not densely) punctate lepidote beneath, although its short (2–4 mm) petiolules match those of the former; its glabrous (except for a few trichomes near margin) calyx is also unlike both of the other plants. This may represent yet a third species whose relationship with *A. parkeri*, another species with glandular-lepidote corolla tube, must be considered.

The Venezuelan plant is now represented by 5 different collections, all of which are quite homogeneous (one lacks foliaceous pseudostipules). Several of these were variously determined (with queries) by Sandwith as *A. carrerense* (= *A. karstenii* Bur. & K. Schum., *Cardona 2868*), *A. parkeri* (*Agostini 386*), and *Pseudopaegma* sp. cf. *P. oligoneuron* (*Killip 37544*) but the relationships seem instead with *A. longidens* and *A. maguirei*.

Anemopaegma patelliforme A. Gentry, sp. nov.

Frutex scandens; ramulis teretibus, sine consociebus glandularum in nodis inter petioles; folia trifoliolata vel bifoliolata cum cirrho, foliolis ovatis, plerumque glabratis, petiolulis lateralibus 0.8–1.2 cm longis, petiolis 4–10 cm longis; inflorescentia racemosa, axillaris brevis; calyx patelliformis, truncatus, puberulus; corolla aurata, tubulo-campanulata, tubo lepidoto; ovarium oblongo-ellipticum, lepidotum, basaliter contractum; discus pulvinatus; capsula ignota.

Liana; branchlets terete, finely striate, glabrate; interpetiolar glandular fields absent; pseudostipules spathulate-foliaceous, to 5 mm long, 2 mm wide, caducous. Leaves 3-foliolate or 2-foliolate with a simple (?) tendril; leaflets ovate, acute to acuminate, the base rounded to very broadly cuneate, 10–15 cm long, 5–7.5 cm wide, membranaceous to chartaceous, the main veins slightly raised above, prominent below, scattered impressed-lepidote, otherwise mostly glabrous, usually with a few minute inconspicuous trichomes scattered along main vein above and below, with conspicuous clusters of plate-shaped glands in axils of lateral nerves below, drying olive; lateral petiolules 0.8–1.2 cm long, the terminal petiolule to 3.5 cm long; petioles 4.0–10 cm long, puberulous. Inflorescence a short 4–7-flowered axillary raceme, the pedicels and rachis puberulous. Flowers with the calyx expanded-campanulate, truncate, ca. 3 mm long, 6–8 mm wide, minutely puberulous, with plate-shaped glands in upper half; corolla yellow, tubular-campanulate, 4.3–5.2 cm long, 1.4–1.7 cm wide at mouth of tube, the tube 3.5–4 cm long, the lobes 0.7–1.1 cm long, glandular lepidote outside, the lobes mostly glabrous, with a few trichomes along the subciliate margins, the tube inside mostly glabrous, with some glandular-lepidote scales, densely pubescent at level of stamen insertion; stamens didynamous, the anther thecae divaricate, 3 mm long, the longer filaments 1.8–1.9 cm long, the shorter filaments 1.4–1.6 cm long, the staminode 4–5 mm long, insertion 9–10 mm from base of corolla tube; pistil ca. 2.5 cm long, the ovary oblong-elliptic, 2 mm long, 1 mm wide, contracted slightly at base, densely glandular-lepidote, the ovules 4-seriate in each locule in cross section; disc pulvinate, tapering to base of ovary, ca. 1 mm long, ca. 2 mm wide. Capsule unknown.

TYPE: VENEZUELA. AMAZONAS: Mavaca, Alto Orinoco, Indios Guaicas (Yanomano), las flores son utilizadas para adorno en las orejas perforadas de las mujeres, trepadora de flores amarillas, Jan. 1970, *Aristeguieta & Lizot 7374* (VEN, holotype; MO, fragments).

Vegetatively this plant is similar to *A. longipetiolatum* Sprague of Paraguay because of its long petioles. That species is very different in puberulous leaves, much larger narrowly campanulate calyx, and longer inflorescence. The calyx of *A. patelliforme* is reminiscent of that of *Arrabidaea* (*Petastoma*) *patellifera* (Schlecht.) Sandw. and matched in *Anemopaegma* only by very different pubescent-leaved *A. oligoneuron* (Sprague & Sandw.) A. Gentry and by *A. insculptum* (Sandw.) A. Gentry. The latter, perhaps the closest relative of *A. patelliforme*, lacks lepidote scales on the outside of the corolla as well as having shorter (3–5 cm long) petioles and longer (1.5–2 cm long) lateral petiolules. *Anemopaegma insculptum* also differs in having interpetiolar glandular fields and lacking glandular fields in the axils of the lateral nerves below.

Anemopaegma villosum A. Gentry, sp. nov.

Frutex scandens; ramuli teretes, villosi, sine consociebus glandularum in nodis inter petioles; pseudostipulis foliaceis; folia 2-foliolata, foliolis ellipticis, acutis, subtus villosis; inflorescentia floribus 1–3 in axillis foliorum dispositis; calyx cupulatus, fere membranceous, truncatus; corolla tubulo-campanulata, tubo extus lepidoto; stamina thecis divaricatis; ovarium ellipsoideum, lepidotum; discus pulvinatus; capsula ignota.

Vine; branchlets terete, finely striate, villous; interpetiolar glandular fields absent; pseudostipules thinly foliaceous, elliptic, acute, 5–15 mm long, 2–8 mm wide, noticeably veined. Leaves 2-foliolate, often with a minutely trifid tendril; leaflets ovate, acute to short-acuminate, rounded to truncate at base but often abruptly attenuate at top of petiole, 6.5–9 cm long, 3.5–5.5 cm wide, membranaceous, pubescent with scattered trichomes above, villous beneath, especially along main veins, the trichomes to almost 1 mm long, drying olive; petiolules 1.5 cm long; petioles 2 cm long, villous. Inflorescence 1–3 axillary or terminal flowers, the pedicels pilose, 4–7 mm long. Flowers with the calyx cupular, almost membranaceous, truncate, 5–6 mm long, 5 mm wide, appressed-pilose, eglandular; corolla "yellow with white," tubular-campanulate, 4.5 cm long, 1.4–2 cm wide at mouth of tube, the tube 4 cm long, the lobes ca. 0.7 cm long, conspicuously glandular-lepidote outside and on lobes and upper part of tube inside, sparsely pubescent at level of stamen insertion; stamens didynamous, inserted 6–7 mm above base of corolla tube, the filaments 1.5–2 cm long, the anther thecae divaricate, 3 mm long; ovary ellipsoid, slightly narrowed at base, 2 mm long, 1 mm wide, densely minutely lepidote; disc conical pulvinate, 1 mm long, 1.5 mm wide. Capsule not known.

TYPE: VENEZUELA. PORTUGUESA: Selva tropófila sobre peñasco calcáreo, 5 km este-noreste de Agua Blanca 22 km noreste de Acarigua, 190 m, twining around shrubs on bluffs, corolla yellow with white, leaves membranaceous, gray green below, 24 Aug. 1966, *Steyermark & Rabe 96455* (VEN, holotype; NY, US, isotypes).

This species is most closely related to *A. rugosum* (Schlecht.) Spr. which differs in conspicuously bullate leaflets, obtuse pseudostipules, a more coriaceous calyx, and especially a pilose indumentum of stiff erect trichomes on leaves and branchlets. *Anemopaegma rugosum* is known only from altitudes of 600–1,300 m in Distrito Federal and Aragua State.

SANHILARIA & PARAGONIA

Paragonia brasiliensis (H. Baill.) A. Gentry, comb. nov.

Sanhilaria brasiliensis H. Baill., Hist. Pl. 10: 27. 1888 (1891).

Examination of the type specimen of Baillon's monotypic genus indicates that it is very similar to *Paragonia pyramidata* (L. Rich.) Bur., the only species of *Paragonia*. There can be no doubt that *Sanhilaria* and *Paragonia* are synonymous. The question which must be resolved is whether *Sanhilaria brasiliensis* is even specifically distinct from *P. pyramidata*.

The type collection of *S. brasiliensis*—*St. Hilaire 745* (P) from Minas Gerais, Brazil—has all essential characters of *Paragonia*, including the characteristic subulate pseudostipules. It differs from *P. pyramidata* in its softly puberulous short-petioled leaves, narrower inflorescence, and especially in the conspicuously costate almost winged calyx; no corollas are extant. A second sheet of the same collection has an immature fruit which is more compressed than in *P. pyramidata* and lacks the characteristic sandpaperlike surface of that species. The fruit of *Sanhilaria* is densely lepidote. Another collection of *Sanhilaria* is now at hand (*Heringer 10277*, Jequié, Bahia, Brazil (NY)) and has corollas exactly like those of *P. pyramidata* except for the acute corolla lobes. This collection has glabrous leaflets but the leaves are otherwise similar to those of the type in their small size, narrowly elliptic shape, and very short petioles and petiolules. A third collection of *Sanhilaria*, also from Bahia (Serra da Agua de Rega, 28 km N of Seabra, 1000 m, *Irwin et al. 31159* (MO)), was originally misidentified by me as *Adenocalymma* sp. This collection is in young fruit and the fruits are densely lepidote, smooth-surfaced, and strongly compressed. The characteristic costate calyx is persistent on one of them. The leaflets of the Irwin et al. collection are glabrous (except for lepidote scales) as in the Heringer collection and have the characteristic narrowly elliptic shape and blunt apex of *Sanhilaria*. As in the other two *Sanhilaria* collections, the petioles and petiolules are extremely short to essentially nonexistent.

Paragonia pyramidata also occurs in Brazil ranging southward to Rio Grande do Sul. However, I have seen no collection of *P. pyramidata* which approaches *Sanhilaria* in leaf form, the species differing constantly in having much longer petioles and petiolules and a wider ovate or elliptic-ovate leaflet. *Paragonia pyramidata* is known from Goias and the Distrito Federal where it typically has its leaves softly puberulous below as in the type of *Sanhilaria*. I regard such variation in pubescence as taxonomically unimportant. Collections of *P. pyramidata* from Brazil all have the convex sandpaper-surfaced capsule valves, broadly paniculate inflorescences, and ecostate calyces characteristic of the species.

The evidence supports recognition of *Sanhilaria brasiliensis* as a distinct species and the new combination *Paragonia brasiliensis* (Baill.) A. Gentry is necessary.

The two species of *Paragonia* may be separated by the characters listed in Table 1.

Nestoria, Kuhlmannia & Pleonotoma

Pleonotoma albiflora (Salzm. ex DC.) A. Gentry, comb. nov.

Bignonia albiflora Salzm. ex DC., Prodr. 9: 167. 1845. TYPE: Brazil, Bahia, *Salzmann 346* (G-DC, P).
Memora albiflora (Salzm. ex DC.) Miers, Proc. Roy. Hort. Soc. London 3: 185. 1863.
M. obtusifoliolata Bur. & K. Schum. in Mart., Fl. Bras. 8(2): 261. 1896. TYPE: Brazil, Bahia, *Riedel 750* (K, P).
Nestoria obtusifoliolata (Bur. & K. Schum.) Urb., Ber. Deutsch. Bot. Ges. 34: 752. 1916.
N. albiflora (Salzm. ex DC.) Sandw., Candollea 7: 248. 1936.
Kuhlmannia colatinensis J. C. Gomes, Arq. Serv. Florest. 10: 201, *fig. 1*. 1956; Notul. Syst. (Paris) 15: 224, *fig. 2*. 1956. TYPE: Brazil, Espirito Santo, *Kuhlmann 6567* (RB, MO).

TABLE 1. Contrasting features of *Paragonia pyramidata* and *P. brasiliensis*.

P. pyramidata	*P. brasiliensis*
Tendril tip minutely bifid (rarely trifid)	Tendril tip minutely trifid
Petioles and petiolules well developed	Petioles and petiolules reduced, subobsolescent
Leaflets elliptic or ovate-elliptic, the apex obtuse to acuminate	Leaflets narrowly elliptic to oblanceolate, the apex obtuse
Calyx ecostate	Calyx conspicuously ridged (cf. *Fridericia*)
Inflorescence broadly paniculate	Inflorescence racemose-paniculate
Capsule subterete, sandpaper-surfaced	Capsule strongly compressed, smooth-surfaced, densely lepidote (immature)
Corolla lobes rounded	Corolla lobes acute
Mexico to southern Brazil	Eastern Brazil (Bahia and Minas Gerais)

The monotypic genus *Nestoria* was segregated from *Memora* by Urban (1916) on the basis of its trifid tendril and tricolpate pollen. Bureau & Schumann (1896–1897) had earlier suggested that its single species seemed out of place in *Memora* because of its *Anemopaegma*-like flower and open inflorescence. Sandwith (1936) pointed out that the pollen and tendril characters used by Urban to segregate *Nestoria* were just those of *Pleonotoma* which likewise has biternate leaves and similar white or cream corollas. However, he retained *Nestoria* as rather doubtfully distinct from *Pleonotoma* on the basis of its many-ribbed rather than tetragonal branchlets and its "remarkable inflorescence." These characters are insufficient for generic segregation in my opinion.

The Salzmann type collection of *Nestoria albiflora* does have conspicuously tetragonal branchlets with the four angles ribbed and contrastingly lighter colored than the rest of the branchlet. This tetragonal branchlet is readily visible even in the Field Museum photograph (negative 7674) of the type and is just that of *Pleonotoma*. The Salzmann collection is obviously very close to *Pleonotoma*. On the other hand the Riedel type collection of *Memora obtusifoliolata* has mostly very inconspicuously, or not at all tetragonal, 6–8-ribbed branchlets. Only above the nodes are the branchlets of this collection clearly tetragonal. The calyces of this collection are also somewhat shorter than those of the Salzmann collection and the leaflets are round-tipped. Nevertheless, the two collections are so similar as to leave little doubt that they are conspecific.

Now we must remember that neither Schumann (collaboration with Bureau being purely nominal) nor Urban had seen the Salzmann collection. *Memora obtusifoliolata* was described from the Riedel collection as having terete branchlets, thus seeming to accord with *Memora* in this important aspect. When Urban surveyed pollen and tendrils of the Bignoniaceae, he discovered that *M. obtusifoliolata* differed from other members of *Memora* as noted previously and consequently erected the monotypic *Nestoria* for it. We may presume that had these

authors seen the more tetragonal-stemmed Salzmann collection they might have recognized its affinity with *Pleonotoma*, especially as that genus has both the trifid tendrils and 3-colpate pollen which led to Urban's rejection of the species from *Memora*.

Meanwhile Miers, who had seen the Salzmann collection, had transferred *Bignonia albiflora* to *Memora* rather than to *Pleonotoma* despite the tetragonal branchlets. This is hardly surprising when one remembers that *Memora* and *Pleonotoma* were defined very differently by Miers than by subsequent authors with foliaceous pseudostipules as the major diagnostic character. Species with terete stems and simple tendrils were thus lumped with unrelated species having tetragonal branchlets and trifid tendrils.

We have, then, a species known from two collections, one with quite obviously tetragonal branchlets, the other with 6–8-ribbed subtetragonal or subterete branchlets. We also know that several accepted species of *Pleonotoma* may have inconspicuously tetragonal and even multi-ribbed (though with four ribs more conspicuous) older branchlets. How fundamental is the difference between tetragonal and multi-ribbed branchlets? Evidence from other genera indicates that in several species of Bignoniaceae normally having tetragonal, 4-ribbed branchlets [e.g., *Mussatia hyacinthina* (Standl.) Sandw., *Cydista diversifolia* (H.B.K.) Miers], occasional plants or branches of plants may be perfectly 6-angled and 6-ribbed. The change from 4-angled to 6-angled may be reversed or repeated even on a single branch. Whereas ribbed and angled branchlets may differ fundamentally from unribbed terete ones, the number of ribs is less important, even in species delimitation. The ribbed branchlets of *Nestoria* ally it with *Pleonotoma*.

The inflorescence of *Nestoria* is a very lax open raceme while the typical inflorescence of *Pleonotoma* is a relatively few-flowered and contracted raceme with a different facies. However, such species of *Pleonotoma* as *P. clematis* (H.B.K.) Miers, *P. melioides* (S. Moore) A. Gentry, or *P. jasminifolia* (H.B.K.) Miers may have inflorescences ranging in size from a few flowers to an elongate 18-or-more-flowered raceme with successive flower pairs separated by 3 cm and pedicels at least 2.5 cm long. The inflorescences of these species have exactly the same appearance as that of *Nestoria*.

Additional evidence also supports the affinity of *Nestoria* with *Pleonotoma*. While the tetragonal branchlets of *Pleonotoma* have received all the taxonomic attention, the petioles and petiolules of *Pleonotoma* are also characteristically tetragonal with raised angles. The petiolules (and sometimes the petioles) of *Nestoria*, even in specimens with subterete branchlets, are sharply tetragonal with raised angles just as in *Pleonotoma*.

Another kind of evidence comes from an unexpected source: examination of type material of *Kuhlmannia colatinensis* proves that monotypic genus synonymous with *N. albiflora*. The *Kuhlmannia* type includes the first known fruit of *Nestoria* and this fruit is also similar to that of some species of *Pleonotoma*.

All available evidence (trifid tendril, 3-colpate microreticulate pollen, biternate leaves, inflorescence, flowers, ribbed subtetragonal branchlets, fruit) supports merger of *Nestoria* (and *Kuhlmannia*) with *Pleonotoma*. The single new

combination *Pleonotoma albiflora* (Salzm. ex DC.) A. Gentry reduces two unnecessary and monotypic genera to synonymy.

This rare species has been assumed endemic to eastern Brazil (Bahia and Espirito Santo) so the discovery of a disjunct population in lowland Guyana is entirely unexpected. Nevertheless, I am unable to distinguish from *P. albiflora* a suite of specimens from Venezuela, Surinam, French Guiana, and Amapa, Brazil. Amazingly, the collection from French Guiana was made by Aublet long before the first Brazilian collections. Guyana area collections I have examined are: VENEZUELA. DELTA AMACURO: Río Grande cerca de los límites del Estado Bolívar, *Blanco 498* (VEN). SURINAM: Mapanegebied, Kamp 8, *Vreden 11320* (WAG). FRENCH GUIANA: without locality, *Aublet s.n.* (BM). BRAZIL. Rio Jarí (border of Amapa and Para), Água Branca, *Silva 2459* (IAN). A sterile collection from Amazonas, Brazil [*Gentry & Ramos 13333*, km 120, Manaus-Itacoatiara Road (MO, INPA)] may be a juvenile form of this species.

Two of these collections are in fruit, permitting amplification of Gomes's fruit description. The fruit of *P. albiflora* is linear-oblong, flattened but with rather woody valves, glabrous, 35–51 cm long, 2.1–3 cm wide, acute at base and apex, drying light green. The seeds are very thin, bialate, ca. 1.8 cm long and 7.5 cm wide, drying uniformly brownish except for very narrow hyaline wing tips. The seeds are uniseriate as in *Memora* but unlike other species of *Pleonotoma*. This difference is inadequate for generic segregation of *Nestoria*.

XEROTECOMA & GODMANIA

Godmania dardanoi (J. C. Gomes) A. Gentry, comb. nov.

Xerotecoma dardanoi J. C. Gomes, Rev. Bras. Biol. 24: 405. 1965. TYPE: Brazil, Pernambuco, *Lima 61-3598* (RB).

Gomes compared his monotypic new genus with *Tabebuia* (*Tecoma* to him) because of its arboreous habit, 3-colporate reticulate pollen grains, and palmately compound leaves. He separated it from *Tabebuia* because of its striate, spirally twisted capsule, campanulate-gibbous corolla, barbate anthers, and patelliform calyx. Unfortunately, Gomes overlooked the fact that these are the same characters by which *Godmania* is distinguished from *Tabebuia*. Gomes's illustration of *X. dardanoi* also shows such *Godmania*-like features as attenuate leaflets, curved ovary, very short anther thecae, and a seed with an indeterminate irregular-ended wing.

Through the courtesy of the Jardim Botânico of Rio de Janeiro, I was able to examine the type of Gomes's plant during a recent visit to Rio de Janeiro. It proves to match *Godmania* in all essentials. In fact, it is so close to *G. aesculifolia* (H.B.K.) Standl., the only recognized species of the genus, that its specific separation needs to be justified.

Godmania aesculifolia ranges from Mexico to Venezuela and Bolivia and even into extreme northern Brazil (Roraima, Para) but has not been collected south of the Amazon in Brazil. It is thus disjunct from *G. dardanoi* which occurs in the caatinga of eastern Brazil. The corolla of *G. aesculifolia* is considerably smaller (1.0–1.6 cm long) than that of the caatinga plant (2.5–3.0 cm long)

though of the same peculiar shortly and widely campanulate form and with the same unusual short triangular lobes. The 15–38 cm long fruit of the caatinga plant is shorter than the 45–100 cm long fruit of *G. aesculifolia* and the pubescence is of a different consistency. These differences are adequate to maintain the plant of eastern Brazil as specifically distinct and the new combination *Godmania dardanoi* (J. C. Gomes) A. Gentry is in order.

I have seen two additional specimens of *G. dardanoi* besides the type and the two other collections from Pernambuco cited by Gomes. One of these was collected at Santa Elena in Bahia State (*Zehntner 378*, RB 6383); the second (*P. de Campo Porto s.n.*, RB 29630) is without data. Interestingly enough these two collections have been annotated by Kuhlmann with an unpublished manuscript name as a new species of *Godmania*.

Roseodendron & Tabebuia

Tabebuia millsii (Miranda) A. Gentry, comb. nov.

Cybistax millsii Miranda, Bol. Soc. Bot. México 26: 129. 1961. TYPE: Mexico, Chiapas, *Gómez-Pompa 312* (US).
Roseodendron millsii (Miranda) Miranda, Bol. Soc. Bot. México 29: 43. 1965.

A reconsideration of the relationships of *Roseodendron* with *Tabeuia* makes the former's reduction to *Tabebuia* seem advisable, contrary to my former opinion (Gentry, 1970). The two species of this group known to Seibert were placed by him in *Cybistax* (Seibert 1940a, 1940b). Both had been described in *Tabebuia*. They were distinguished from *Tabebuia* by the striate ovary, costate fruit, thin membranaceous calyx, and capitate inflorescence trichomes. These characters were thought to be closer to those of *Cybistax*, a monotypic genus of Central Brazil and adjacent Peru. Miranda subsequently described a third species of the alliance in *Cybistax* as *C. millsii*. Later (Miranda, 1965) he correctly noted that the relationship of these species with *Cybistax* is only superficial. He erected for them the new genus *Roseodendron*, separated from *Cybistax* by the more delicately membranaceous, narrower, ecostate calyx, narrowly oblong, estipitate ovary, and indumentum of branched trichomes and lepidote scales with raised borders. He might also have mentioned *Roseodendron*'s much narrower linear fruit with relatively inconspicuous ribs, very different from the oblong fruit with narrow, raised, 1–5 mm thick ribs of *Cybistax*.

Clearly *Roseodendron* is much closer to *Tabebuia* than to *Cybistax*. Indeed all of the characters (except calyx texture) noted by Miranda as distinguishing *Roseodendron* from *Cybistax* are also characteristic of *Tabebuia*.

Discovery of the fruits of *Tabebuia guayacan* (Seem.) Hemsl. and *T. capitata* (Bur. & K. Schum.) Sandw. [especially a form of the latter from Peru, *Castillo 37*-MCS (WIS)] lessens the importance of the capsule ribs of *Roseodendron* as a generic character. *Tabebuia capitata* has varyingly striate fruits as does *T. heptaphylla* (Vell.) Toledo (see Gentry, 1975), while *T. guayacan* has irregularly muricate-reticulate or interruptedly costate fruits. Indeed, these fruits can be more costate than that of *Roseodendron chrysea* (i.e., *Tabebuia chrysea* Blake).

Capitate trichomes are a notoriously variable characteristic in Bignoniaceae

and many natural genera (e.g., *Arrabidaea, Lundia, Mansoa, Piriadacus*) have species both with and without capitate trichomes. Their presence in *Roseodendron* does not merit its generic segregation. The thinner calyx of *Roseodendron* is less different from that of *Tabebuia* in fresh material than in the herbarium. In any case it too differs only in degree from the relatively large thin calyces of such *Tabebuia* species as *T. elliptica* (DC.) Sandw. and wet-forest forms of *T. chrysantha* (Jacq.) Nichols. The well-developed central axis of the inflorescence of *Roseodendron* is, in my opinion, a more significant difference from *Tabebuia* than any of those mentioned by Seibert (1940a) but still insufficient for generic segregation. In the field *Roseodendron* has exactly the appearance of *Tabebuia* in flowering, fruiting, or vegetative condition and is routinely recognized by collectors as *Tabebuia.* Even the colloquial names for species of *Roseodendron* are generically the same as those of *Tabebuia*, e.g., in Mexico "macuelís de cerro" for *R. millsii* and "macuelís de bajo" for *T. rosea* (Bertol.) DC. (fide Miranda, 1961).

I now consider *Roseodendron* best treated under *Tabebuia. Tabebuia millsii* is the only new combination needed.

Tabebuia millsii presents another problem. The species has been supposed to be restricted to the Caribbean side of southern Mexico from Veracruz to Chiapas. However, recent collections from central Bolívar State in Venezuela seem indistinguishable from *T. millsii.* The Venezuelan plant agrees with *T. millsii*, rather than *T. donnell-smithii* of Pacific Mexico to El Salvador, in (mostly) 5-foliolate leaves, entire leaflet margins, dense simple pubescence of leaflet undersides, somewhat flattened reticulately veined as well as longitudinally costate fruit, and dimensions of the mature leaf (leaflets to 17 × 7 cm and terminal petiolule 3 cm long; the same dimensions for *T. millsii* are 13 × 6.5 cm and 3 cm, for *T. donnell-smithii* 25 × 14 cm and 7 cm).

In some respects the Venezuelan population is intermediate between *T. millsii* and *T. donnell-smithii.* Its fruit has 8–12 major ribs (compared to 8 in *T. millsii* and 10–12 in *T. donnell-smithii*). Juvenile leaves of the Venezuelan plant (*Marcano-Berti 2560* (VEN), *Gentry & Berry 15060* (MO, VEN)) tend to be 7-foliolate and the leaflets are much larger than mature leaflets and usually somewhat serrate; these juvenile leaves thus approximate the mature leaves of *T. donnell-smithii* (juvenile leaves of *T. millsii* from Mexico are not known). The wood I have seen [*Gentry & Berry 15071* (MO)] is yellow and thus similar to the clear yellow wood of *T. donnell-smithii* rather than to the heavy tough dark wood described by Miranda (possibly in confusion with *T. chrysantha* or *T. guayacan*?) for *T. millsii* in Mexico. However, lumbermen around La Paragua at the eastern edge of the range of the Venezuelan plant claim that trees from further west have a much darker wood.

Despite its long disjunction, I cannot separate the Venezuelan population from the Mexican one. The only consistent difference between the Venezuelan and Mexican populations of *T. millsii* is in their fruits (based on a single fruiting collection of each). The Venezuelan fruits are only 1.4–2.1 cm wide while those of Mexican *T. millsii* are 2.1–3 cm wide and those of *T. donnell-smithii* are (fide Seibert, 1940a) 2–3 cm wide. The Venezuelan fruits have mostly simple eglandular trichomes while those of *T. millsii* have gland-tipped and dendroid trichomes.

However, the Venezuelan fruits do have occasional branched and gland-tipped trichomes and the difference in capsule width does not warrant a taxonomic distinction. Long range disjunctions are not uncommon in Bignoniaceae (although often collecting artifacts) but in no other case known to me does a disjunction involve such limited areas of distribution at both ends. *Tabebuia donnell-smithii* is introduced in Ecuador and one wonders if a similar introduction might have taken place in Venezuela. However, the Venezuelan tree, known locally as "cacho de venado," is certainly native and is in fact one of the three major timber trees of the La Paragua area (along with "cedro" (*Cedrella*) and "laurel" (*Cordia alliodora*)).

It seems probable that the morphologically somewhat intermediate Venezuelan population represents the ancestral form for both Mexican plants with differentiation of *T. donnell-smithii* in western Mexico and minor changes in *T. millsii* in eastern Mexico occurring subsequent to disruption of a once more continuously distributed ancestral stock.

Distictis & Distictella

Distictis pulverulenta (Sandw.) A. Gentry, comb. nov.

Distictella pulverulenta Sandw., Brittonia 3: 91. 1938. TYPE: Brazil, Amazonas, *Krukoff 8685* (BM, BR, GH, F, K, MO, NY, U).

My recent treatment of *Distictis* (Gentry, 1974d) concluded that several closely related genera (*Phaedranthus*, *Anomoctenium*, *Wunschmannia*) should not be segregated from it. One other genus also needs to be considered in relation to *Distictis*. This is *Distictella*, a segregate which agrees with *Distictis* in large-meshed (alveolate) acolpate pollen, trifid tendrils, phloem 4-armed in stem cross section, a more or less racemose, usually bracteate inflorescence with large tubular flowers, campanulate, truncate cupular calyx, conspicuous disc, and flattened ovoid woody fruit.

Bureau (1864) was the first to propose the separation of *Distictis* (as *Macrodiscus*) from *Distictella* (as *Distictis*). *Distictella* (his *Distictis*) was characterized by the ovary containing a number of series of ovules in each locule and surmounting a cylindrical disc, an oblong, tomentose, flattened capsule with two woody curved valves (one concave, the other convex), the tip of the replum attached to the septum which bears numerous series of linear seed scars along each border, and pubescent seeds. *Distictis* (his *Macrodiscus*) was said to differ from the preceding by the glabrous uncurved capsule with a furrow in place of a rib on each valve, free replum ends extended beyond the tip of the septum, glabrous seeds, and a punctiform hilum; all these characters are those of the fruit. Urban (1916) later pointed out that Bureau had misapplied *Distictis* and that *Macrodiscus* was actually *Distictis* while *Distictis* sensu Bureau must be known as *Distictella*.

Schumann (1894) introduced new characters in separating *Distictis* (as *Macrodiscus*) from *Distictella* (as *Distictis*) on account of its thinner corolla without a conspicuous bend in it. He also noted that *Distictella* differs from *Pithecoctenium* in having terete twigs lacking the detachable ribs of the latter's

TABLE 2. Real and supposed differences between *Distictis* and *Distictella*.

Distictis	*Distictella*
Capsule glabrous	Capsule pubescent
Capsule not curved	Capsule curved
Capsule midline impressed	Capsule midline raised (implied)
Ends of replum free and extended beyond end of septum	Ends of replum attached to end of septum
Seed scars punctiform	Seed scars linear
Seeds glabrous, with relatively short wings	Seeds pubescent with longer wings
Corolla thinner in texture	Corolla thicker in texture
Corolla straight or slightly curved	Corolla strongly bent
Branchlets 6-angled and ribbed	Branchlets terete, not ribbed

6-angled twigs. Melchior (1927) did not consider *Distictis* in his synopsis of subtribe Pithecoctineae but considered this character of taxonomic importance, separating *Distictella* from *Neves-Armondia* and *Pithecoctenium* on the basis of round rather than 6-angled branchlets. Sprague & Sandwith (1932) further emphasized the character of absence of detachable ribs in *Distictella*. Although considerations of terete versus angled and ribbed branchlets were intended to apply to *Distictella* as compared with *Pithecoctenium*, they are equally valid to separate it from *Distictis*.

The differences that have been proposed to separate *Distictis* (sensu stricto) and *Distictella* are listed in Table 2.

A number of new species have been discovered in both genera since these generic differences were outlined by Bureau (1864) and Schumann (1894) and the fruit differences prove not to be correlated with the floral and vegetative characters. For example *Distictis gnaphalantha* (A. Rich.) Urb. has pubescent fruits but is certainly congeneric with *Distictis lactiflora* (Vahl) DC., the type species of *Distictis*. *Distictella obovata* Sandw. and *D. monophylla* Sandw. have the flowers and twigs of *Distictella* but the fruit of *Distictis* (fruits with scarcely or not at all evident midrib, acuminate, the valves not curved, seeds glabrous). My (Gentry, 1974d) reduction of *Anomoctenium*—which agrees with *Distictis* in uncurved fruit, 6-angled branchlets, and nearly straight corolla—to *Distictis* has expanded that genus to include species with pubescent seeds.

In general the characters of the fruit elucidated by Bureau lack taxonomic significance at the generic level. Seed scars vary considerably in shape even within a single species and the "punctiform" seed scars of *D. lactiflora* are not fundamentally different from the "linear" seed scars of *Distictella*; indeed Bureau's own illustration of *Distictis* (as *Macrodiscus*) showed elongate rather than punctate seed scars. The ends of the replum are extended beyond the end of the septum in species of both genera which have acuminate fruits but not in those species with apically blunt fruits. A tendency to seed pubescence is found in

several species of *Distictis* while some species of *Distictella* have glabrous seeds. The capsule midline may be raised or not and the capsule curved or not in *Distictella*; the capsule is usually pubescent in *Distictis* as well as *Distictella*.

We are left with only vegetative and floral characters separating the two genera. With the exception of a single species these characters appear to be constant and correlated. The flowers of *Distictella* (with one exception) match the syndrome of xylocopid (or *Pithecoctenium*-type) flowers (Gentry, 1974b) in having a thickened corolla which is strongly bent near the middle. With a single exception, these flowers are white, usually with a yellow throat. The flowers of *Distictis* are somewhat thinner in texture and more or less straight. Most are of the "*Anemopaegma*-type" and are adapted for generalized bee pollination. These species have corollas ranging in color from cream to lavender or magenta. Two species of *Distictis* have the corolla deeper red, more elongate, and stamens exserted or subexserted; these are adapted to hummingbird pollination. All species of *Distictis* have 6-angled branchlets with the angles ribbed; all species of *Distictella* (with one exception) have terete unribbed branchlets. Otherwise there appears to be no vegetative difference.

There are several exceptions to the characters noted above for *Distictella*. Happily enough a single species is responsible for all the exceptions: *Distictella pulverulenta* Sandw. has ribbed 6-sided branchlets, a straight corolla, and flowers described as rich purple. *Distictella pulverulenta* is actually a *Distictis* and the new combination *Distictis pulverulenta* (Sandw.) A. Gentry is necessary. *Distictis pulverulenta* becomes the tenth species of *Distictis* (see Gentry, 1974d).

Should the rest of the species of *Distictella* remain segregated from *Distictis*? The removal of *D. pulverulenta* leaves *Distictella* as a homogeneous and well-circumscribed group. While its nearest relationships are clearly with *Distictis*, it is convenient, at least provisionally, to accept the now traditional separation of *Distictella* while noting that the fruit characters on which this segregation was originally based are of minimal value.

Literature Cited

Bureau, E. 1864. Monographie des Bignoniacees. Bailliere et fils, Paris.

——— & K. Schumann. 1896–1897. Bignoniaceae. *In* C. F. P. Martius (editor), Flora Brasiliensis 8(2): 1–452.

Dugand, A. 1946. Noticias Botanicas Colombianas VI. Caldasia 4: 51–65.

Gentry, A. H. 1970. A revision of *Tabebuia* (Bignoniaceae) in Central America. Brittonia 22: 246–264.

———. 1973. Generic delimitations of Central American Bignoniaceae. Brittonia 25: 226–242.

———. 1974a (1973). Bignoniaceae. *In* R. E. Woodson & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 60: 781–977.

———. 1974b. Coevolutionary patterns in Central American Bignoniaceae. Ann. Missouri Bot. Gard. 61: 728–759.

———. 1974c. Studies in Bignoniaceae 12: New or noteworthy species of South American Bignoniaceae. Ann. Missouri Bot. Gard. 61: 872–885.

———. 1974d. Studies in Bignoniaceae 11: A synopsis of the genus *Distictis*. Ann. Missouri Bot. Gard. 61: 494–501.

———. 1975. Identification of Vellozo's Bignoniaceae. Taxon 24: 337–344.

———. 1976. Notes on S. Moore's Mato Grosso Bignoniaceae. Ann. Missouri Bot. Gard. 63: 42–45.

GOMES, J. C. 1955. Contribucão a sistematica das Bignoniaceae Brasileiras. Arq. Serv. Florest. 9: 261–296.
HUNT, D. R. 1972. A note on the typification of *Adenocalymma marginatum* (Bignoniaceae). Kew Bull. 27: 335–336.
MELCHIOR, H. 1927. Der natürliche Formenkreis der Pithecocteniinae innerhalb der Familie der Bignoniaceae. Repert. Spec. Nov. Regni Veg. Beih. 46: 71–82.
MIRANDA, F. 1961. Plantas nuevas del sur de México. Bol. Soc. Bot. México 26: 129–132.
———. 1965. Estudios acerca de arboles y arbustos de México. Bol. Soc. Bot. México 29: 42–48.
SANDWITH, N. Y. 1936. Identification of certain Candollean types of South American Bignoniaceae. Candollea 7: 244–254.
———. 1947. *Bayonia* Dugand. Kew Bull. 1946: 87–88.
———. 1955. Studies in Bignoniaceae XX. Kew Bull. 1954: 597–614.
SCHUMANN, K. 1894. Bignoniaceae. *In* A. Engler & K. Prantl (editors), Natürlichen Pflanzenfamilien 4(3b): 189–252.
SEIBERT, R. J. 1940a. The Bignoniaceae of the Maya Area. Publ. Carnegie Inst. Wash. 522: 375–434.
———. 1940b. New names in *Cybistax* and *Tabebuia*. Trop. Woods 63: 7–8.
SPRAGUE, T. A. & N. Y. SANDWITH. 1932. The *Tabebuias* of British Guiana and Trinidad. Kew Bull. 1932: 18–28.
STANDLEY, P. C. & L. O. WILLIAMS. 1974. Bignoniaceae. *In* Flora of Guatemala. Fieldiana 24(10): 153–232.
URBAN, I. 1916. Über Ranken und Pollen der Bignoniaceen. Ber. Deutsch. Bot. Ges. 34: 728–758.

INFLORESCENCE UNITS IN THE CYPERACEAE[1]

LIENE TEIXEIRA EITEN[2]

ABSTRACT

A classification of ultimate inflorescence units in the Cyperaceae is proposed, establishing six groups. It is concluded that there is no evidence for considering: (1) the rachilla of the *Cyperus*-, *Scleria*- or *Rhynchospora*-type of spikelet to be sympodial; (2) nor the apparently simple flowers in the Cypereae, Scirpeae, and Rhynchosporeae to be pseudanthia; (3) nor the female flower in *Scleria* to be terminal; (4) nor the rachilla of the female flower-bearing spikelet in the Cariceae to be sympodial. Evidence is presented which throws doubt on the concept that *Scleria* is related to the *Diplacrum-Bequerelia* group of genera, and other evidence is presented which shows that the apparently terminal female flower in the Lagenocarpeae is really lateral.

One of the most important characteristics to be considered in dividing the Cyperaceae into subfamilies, tribes, and subtribes is the branching pattern of the ultimate branch orders of the inflorescence. As a result of 15 years' experience examining thousands of specimens, I present a new classification of these branching patterns. Six groups are distinguished which it is believed will account for all the genera of the family. Brazilian genera are mentioned as examples for each group; a few non-Brazilian genera (marked with asterisks) are also given when these are such that they extend the range of character variation which each group may contain.

Since the inflorescence units are extremely contracted and the internodes very slightly developed, the analysis of the branching patterns was based on the following morphological principles:

1. A stem arises from a stem in the axil of a leaf. In a few cases the subtending leaf may be absent. In the aerial part of the plant, the culm, culm branch, rachis, branches from the rachis, rachilla, and flower axis are successively higher branch orders of the stem, while bract, glume, glumella, scale, prophyll, utricle (perigynium), and some kinds of bristles are reductions and modifications of the leaf.

2. Leaves arise from stems.

3. A prophyll, recognized by its form and position, indicates the beginning of a new branch. This principle was always helpful when a prophyll was distal but contiguous to a bract. In this case the prophyll does not arise from the same axis as the bract but is really on a new, very short branch which itself arises in the axil of the bract.

4. When two glumes appear to arise at the same level, the one which is really more basal totally or partially surrounds the distal one.

5. The presence of a glumella or a bristle more internally placed than at least one stamen shows that the flowerlike structure in which it occurs is a pseudanthium and not a true flower.

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6. In the angiosperms, flower parts always arise from a floral axis. Therefore, in the Cyperaceae, when a stamen appears to arise directly from the rachilla in the axil of a glume or glumella, it is really on an extremely short floral axis which arises from the rachilla in the axil of the glume or glumella.

In the following discussion of the six groups of ultimate inflorescence units, branching patterns are described, ultimate inflorescence units are defined, and, where necessary, spikelets are defined. The ultimate inflorescence unit may include axes of more than one branch order (not counting in this the floral axes of the lateral flowers, which make still another branch order). A spikelet, however, has only one branch order, the rachilla (besides the floral axes of the lateral flowers).

GROUP I

The axes of the inflorescence terminate in spikelets. The word "spikelet" in this paper is used in the strict sense, that is, a racemosely branched structure consisting of an axis (rachilla) of potentially indefinite growth bearing lateral, true flowers. Each flower arises in the axil of a glume (scalelike bract) which covers it. Besides flower-bearing glumes, empty glumes may be found at the base or at the apex of the rachilla (Fig. 1). A single spikelet may contain all bisexual flowers or both bisexual and male flowers. Very rarely, a taxon is dioecious such as *Cyperus schomburgkianus* Nees var. *leucanthus* (Schrad.) Kük. (Kükenthal, 1935–1936).

In Fig. 1, all the spikelets are shown arising from a rachis in the axil of a subtending bract and, in almost all the genera, the rachilla axis bears a basal prophyll. But in some spikelets of an inflorescence the subtending bract and prophyll may not be present. When a spikelet is lateral and sessile to an inflorescence branch, its subtending bract and prophyll are next to the spikelet and appear to be part of it. However, when the spikelet is terminal on an axis that bears other lateral spikelets, leaves, branches, etc., the subtending bract and prophyll occur at the base of that axis and so are separated from the terminal spikelet. For this reason, the subtending bract and prophyll, and the internode just below and just above the prophyll, are not considered here to be part of the spikelet even when they are next to it.

In *Eleocharis*, the spikelet is always separated from the prophyll of its axis by the length of the culm. In this genus, the leaf from whose axil a culm axis arises is one of the two tubular leaf sheaths of a previous culm. The new culm axis bears its prophyll at its base addorsed to the culm from which it sprang.

Group I consists of the tribes Scirpeae, Cypereae (when this is considered distinct from Scirpeae) and Rhynchosporeae.

Examples of genera in the group are: *Cyperus* (sensu lato), *Remirea*, *Lipocarpha*, *Hemicarpha*, *Ascolepis*, *Androtrichum*, *Fimbristylis*, *Bulbostylis*, *Eleocharis* (including *Chamaegyne* and *Helonema*), *Websteria*, *Egleria*, *Scirpus*, *Fuirena*, *Rhynchospora*, *Dichromena*, *Pleurostachys*, and *Cladium*.

The inflorescence units of *Lipocarpha*, *Hemicarpha*, and *Ascolepis* merit a detailed discussion. They are related genera and have the same habit. Their inflorescences generally consist of 1–3 small ovoid heads each with a thick cen-

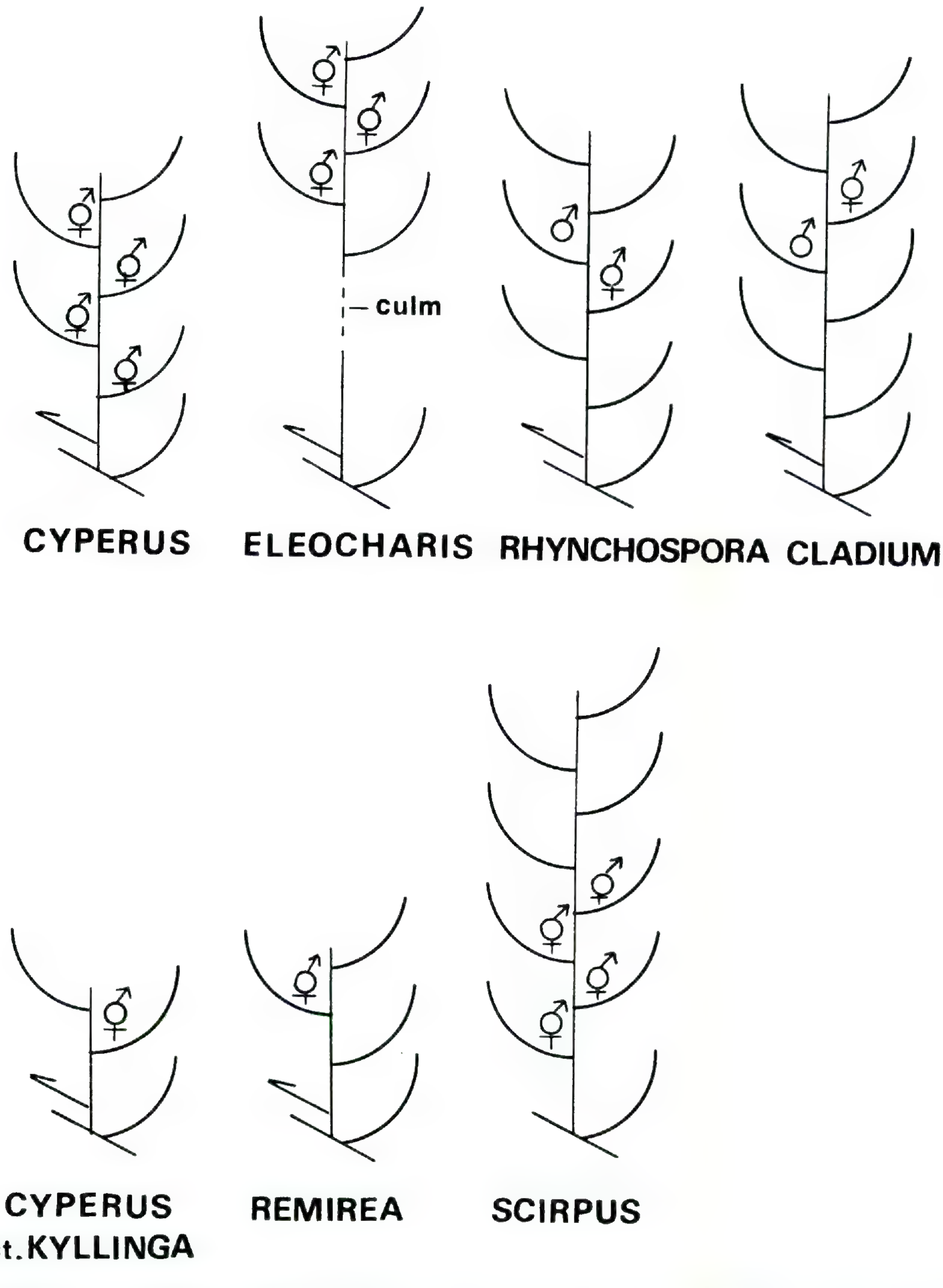


FIGURE 1. Spikelet branching patterns of genera of Group I. Each spikelet is shown with the prophyll (when it has one) of its rachilla axis, the bract from whose axil it arises, and a piece of the lower-order stem from which it branches off. The prophyll and bract are not considered to be part of the spikelet proper. Curved lines represent bracts and glumes, straight lines with hooks represent prophylls. In all diagrams of branching patterns in this paper, a stem axis arising in the axil of a bract is shown slightly separated from the bract symbol in order to show clearly its connection with the mother axis and not with the bract itself. Despite this separation, the branch axis and the subtending bract are considered to arise from the same node. A prophyll is always shown slightly separated from the origin of the axis which bears it in order to make clear from which axis it grows. In this case, the segment from the origin of the axis to the prophyll is a true internode, the subprophyllar internode.

tral rachis. A few species of *Ascolepis*, such as *A. brasiliensis* (Kunth) Bentham ex Clarke, have the same type of heads but other species of the genus, such as *A. capensis* Ridley, have heads with more or less flat compound receptacles as in many Compositae.

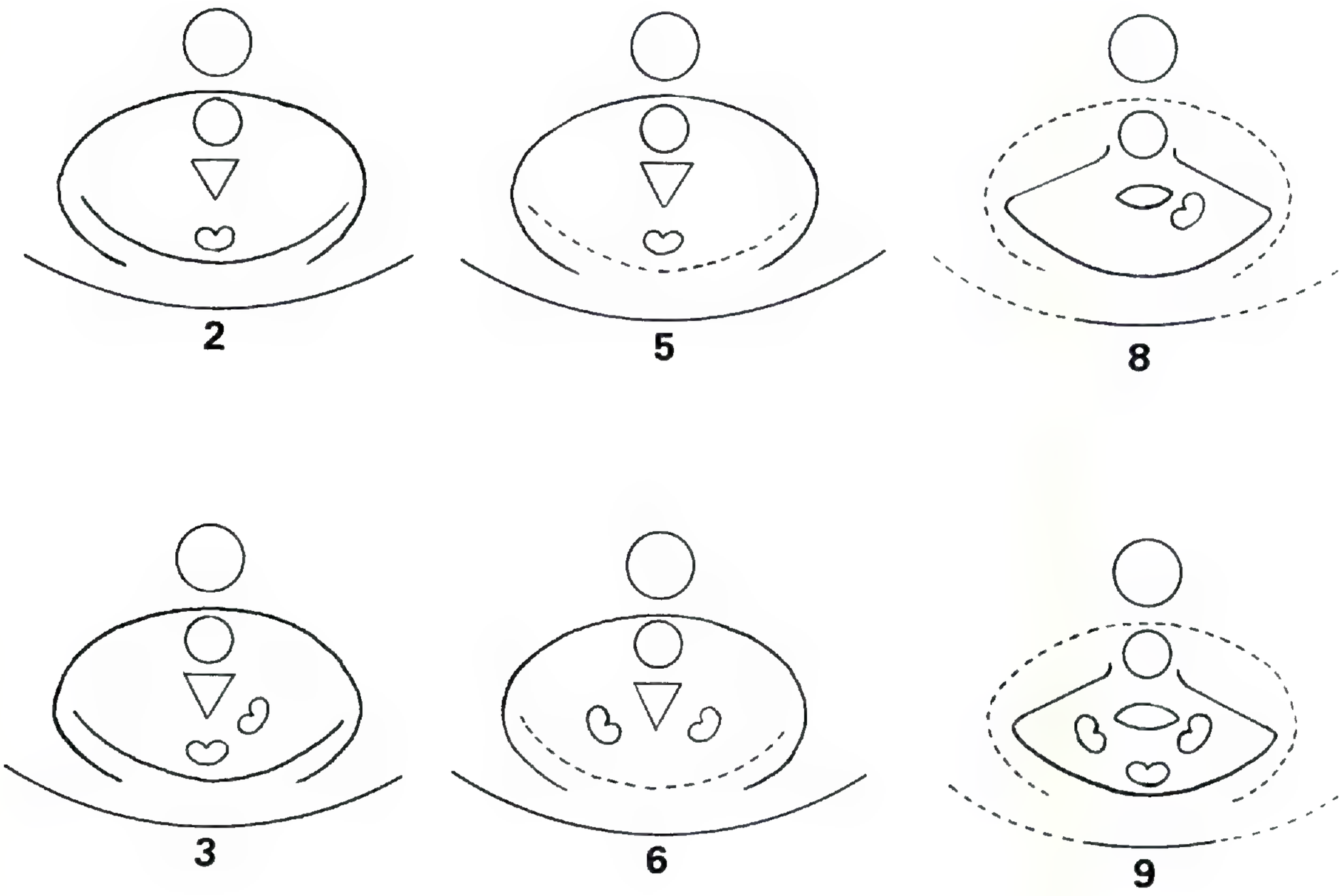
I consider the ultimate inflorescence units in these genera to consist of a bract from whose axil arises a rachilla bearing a single lateral flower. This interpretation is illustrated in Figs. 2–10.

Nees (1842) and Pax (1886) thought that *Ascolepis* (= *Platylepis*), *Hemicarpha, and Lipocarpha* are related to *Hypolytrum* and put these genera in the same tribe, Hypolytreae. Bentham (1883) placed *Ascolepis* with *Hypolytrum* in the tribe Hypolytreae, but also included in this tribe other genera which today are placed in the Mapanieae. To accept Bentham's grouping of these genera means that *Ascolepis* has the same basic structure as the genera of Mapanieae. In the present-day interpretation of the Mapanieae, the axis B bears an apparently terminal pistil which constitutes by itself a unisexual flower, and lateral stamens each constituting a male flower. But *Ascolepis*, as well as *Hemicarpha* and *Lipocarpha*, differs from the Mapanieae in the aspect of the plant and in the inflorescence. These three genera are very similar in habit to species of *Cyperus* sect. *Kyllinga*, such as *C. sesquiflorus* (Torrey) Mattf. & Kük., *C. densicaespitosus* Mattf. & Kük., and *C. brevicaulis* (Rottb.) Hassk. In herbaria one commonly finds specimens of *Ascolepis* and *Lipocarpha* determined as species of *Cyperus* sect. *Kyllinga*. Compare the drawings of *Lipocarpha*, *Ascolepis*, and *Hemicarpha* in Barros (1947: pars I, tab. XLVIII) and in Kükenthal (1935–1936: fig. 63E).

In *Cyperus* sect. *Kyllinga*, the spikelet often has only a single flower. The branching pattern in this case is given in Fig. 1. It is equal to that of *Lipocarpha* (Fig. 4) with the addition of an empty apical glume. The position of the stamens in *Lipocarpha*, *Hemicarpha*, and *Ascolepis* (Figs. 3, 6, 9) is such that the bisexual flower can be considered to be in the axil of the upper lamina (i.e., the glume) (Figs. 4, 7, 10). This is because in the Cyperaceae in general the stamens occur between the pistil and the glume which subtends the flower.

Another reason to exclude these three genera from the Mapanieae is the absence of the two basal, lateral, pilose-keeled laminas, characteristic of genera of this tribe. In *Lipocarpha*, *Hemicarpha*, and *Ascolepis*, on the contrary, the laminas are parallel to the glumiform bract which subtends the spikelet; these laminas are gently curved (not folded) in cross section and do not possess ciliate keels. For all these reasons, I consider the inflorescence units of these genera to be structures homologous to the one-flowered spikelets of *Cyperus* sect. *Kyllinga*.

In *Lipocarpha* (Fig. 4), beneath the covering bract, there are two thin laminas; the lower (outer) is considered a prophyll and the upper (inner) a glumella which subtends the bisexual flower. In *Hemicarpha* (Fig. 7) the upper lamina (glume) which subtends the flower disappeared in evolution so that the flower appears to be situated between the prophyll and the covering bract. In *Ascolepis* (Fig. 10), the prophyll disappeared and the upper lamina became transformed into the utricle which contains the flower. The sides of this lamina folded in and the margins fused, leaving a subapical orifice on the adaxial side.



FIGURES 2–10. Floral diagrams and branching patterns of inflorescence units of *Lipocarpha*, *Hemicarpha*, and *Ascolepis*, genera of Group I. The triangle and fusiform symbol represent pistils; the reniform symbol, a stamen; the upper circle, the rachis (axis A in the branching patterns); the lower circle, the rachilla (axis B in the branching patterns). The curved lines represent subtending bract, prophyll and glume (the latter called "glumella" in *Lipocarpha* because it is small and thin); the broken-line curve represents parts which have supposedly disappeared in evolution. In the branching patterns, the hooked curves are prophylls; pistil and stamens are also shown.—2–3. Floral diagrams of *Lipocarpha* with 1 and 2 stamens.—4. Branching pattern of *Lipocarpha* inflorescence unit.—5–6. Floral diagrams of *Hemicarpha* with 1 and 2 stamens.—7. Branching pattern of *Hemicarpha* inflorescence unit.—8–9. Floral diagrams of *Ascolepis* with 1 and with 3 stamens. The glume is utriculiform with a subapical adaxial orifice.—10. Branching pattern of *Ascolepis* inflorescence unit. The spikelet proper, as defined in this paper, is, for these three genera, the upper part of the inflorescence unit, that is, the flower, its subtending lamina (glumella in *Lipocarpha*, utricle in *Ascolepis*, none in *Hemicarpha*), and that part of axis B from the insertion of this lamina, distally.

(The floral diagrams in Figs. 8–9 represent the utricle at the level of the orifice.) The utricle is larger and thicker than the homologous organ in the other two genera. Bentham (1883) and Pax (1886) thought that the utricle of *Ascolepis* was formed from two fused laminas. This is not probable because the vascular bundles of the utricle occur only in the abaxial side, so that it is more probable that the utricle is formed of only one lamina. In fact, in a specimen of *Ascolepis* from Zambia (*Richards 18918*,[K]) this lamina does not form a utricle; the margins at the base of the lamina turn in to form a narrow fold but remain free and distant from one another. In the upper portion of this lamina the margins do not even turn in. After having noted that the inflorescence pattern of these three genera is related to that of *Cyperus* sect. *Kyllinga*, I found that Palla (1905) had arrived at essentially the same conclusion.

From the discussion of Group I we see that the ultimate inflorescence unit in the group is of three types: (1) Spikelet (as defined in this paper) alone, when the prophyll and subtending bract of the rachilla axis are not close to the spikelet. (2) Spikelet with the prophyll (when this is present) and the subtending bract of its rachilla axis when these are close to the spikelet, the whole looking like a single unit. Most units found in Group I are of this type and include also the basal spikelets of *Eleocharis* (see discussion of these under *Chamaegyne* in the following paper, Eiten, 1976). (3) Spikelet with its basal associated scale when the latter is not separated from the spikelet by a developed shoot in the axil of this scale (see under *Helonema* in Eiten, 1976). This is found in the culm-tip spikelets of *Eleocharis* and its derived genera, *Websteria* and *Egleria*. In these three genera, when the associated scale is separated from the spikelet by a developed shoot in its axil, the ultimate inflorescence unit is defined as the spikelet only.

In Group I, the definition of the ultimate inflorescence unit in each case makes for a visibly distinct body. (In those species where spikelets are clustered into a head, dissection is necessary to disclose the body but there is no question what parts should or should not be included in each case.) Note that in the two cases where the subtending bract is included in the unit, this necessarily includes the small portion of the rachis axis to which the bract and the rachilla are attached.

In Group I, the spikelet has a monopodial rachilla (Fig. 11a). I cannot agree with those authors from Pax (1886, 1887), Schulz (1887) and Celakovsky (1887) to Mora (1960) and Schultze-Motel (1964) who consider the spikeletlike structure of the Rhynchosporeae to be cymose and its rachilla to be sympodial, that is, that each flower terminates the rachilla internode below it and the next internode is a new branch which also terminates in a flower (Figs. 11b–11c). In this case, the glume which apparently subtends a flower would really subtend the new branch forming the next rachilla internode. These authors therefore call the spikeletlike structure a "partial inflorescence," or "Scheinährchen" (pseudospikelet), not a spikelet. Also, I cannot see any evidence that the Cypereae and Scirpeae are any different from the Rhynchosporeae in this respect, yet Pax and Mora consider the units in these tribes to be true racemose spikelets with monopodial rachillas. (Schultze-Motel considers the spikeletlike units of these tribes

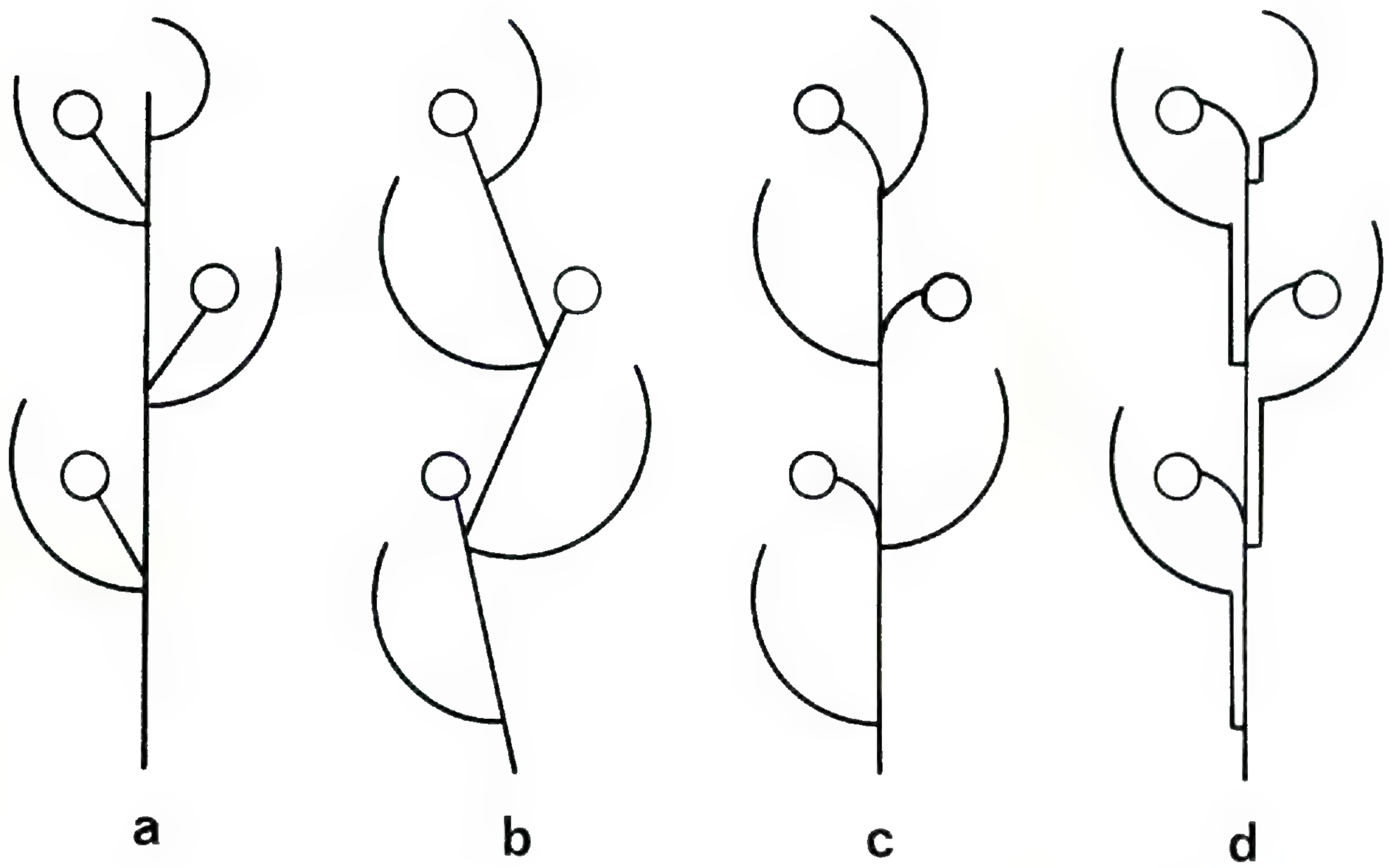


FIGURE 11. Branching patterns of spikelets of Group I under hypotheses of monopodiality and sympodiality.—a. Monopodial rachilla, true spikelet.—b. Sympodial pseudorachilla, scorpoid cyme.—c. Sympodial pseudorachilla with the pseudorachilla straight.—d. Sympodial pseudorachilla with recaulescence (adnation) of basal part of each glume to the axis which it subtends.

also to be cymose.) Mora says the decisive indication is whether the rachilla has a terminal flower at its tip or not; if it does, the structure is cymose (i.e., the rachilla is sympodial). As will be seen in various parts of this and the following paper (Eiten, 1976), an apparent terminal position of a flower in the Cyperaceae is no indication that it really is so; rather, it may well be pseudoterminal, that is, lateral.

In an inflorescence of the type supposed by Pax, Schulz, Celakovsky, Mora, and Schultze-Motel to be a scorpoid cyme,[3] each glume would be on the opposite side of the stem from the flower (Figs. 11b–11c). (The same would be true for the helicoid cyme in Schultze-Motel's conception of the inflorescence unit of the Scirpeae.) Since the glumes are really on the same side of the rachilla as their flowers, appearing to subtend them, this is explained by assuming recaulescence

[3] These authors invariably call this cyme a "Fächel" (rhipidium), which is a scorpoid cyme with all its branches lying in one plane. The branches, each terminating in a flower, in the distichous spikelets of the Cypereae do lie in one plane, but those of the Scirpeae and Rhynchosporeae do not since the flowers in these tribes are spirally arranged. To be consistent with their concept of a cymose structure, these authors should call the units in these two tribes a "Wickel" (cincinnus). Schultze-Motel (1964) considers the spikeletlike structure of the Rhynchosporeae and Cypereae to be a rhipidium also, but that of the Scirpeae he calls a "Schraubel" (bostryx), which is a helicoid cyme with the consecutive branches all arising on the same side and each lying at a transverse or oblique angle to its predecessor, not in the same plane. (Its diagram would be like Figs. 11b–11c, but with all the flowers on the same side of the rachilla.)

(Troll, 1964: 127), that is, adnation or concrescence of the basal part of the glume to the next internode, in this case to the supposed new branch that arises in the axil of the glume (see figure in Celakovsky, 1887). The adnate part of the glume is assumed to be narrow so that with the rachilla segment it would look like a single stem. The free part of the glume would then be on the same side of the axis as the *following* flower, appearing to subtend it (Fig. 11d).

I examined cross and longitudinal sections of the spikelets of three species of *Rhynchospora* and a species of *Cyperus*. (*Rhynchospora* sp.: *Hatschbach 14942*, Brazil, Paraná, Mun. Bituruna, 17 Oct. 1966. *Rhynchospora* sp.: *Hatschbach 14824*, Brazil, Paraná, Mun. Piraquara, 10 Oct. 1966. *Rhynchospora corniculata* (Lam.) A. Gray: *Swayne & Bailey 1112*, U.S.A., Illinois, Gallatin Co., 3 Aug. 1950. *Cyperus* sp.: *Robinson 6192*, Zambia, Chakwenga Headwaters, 100–129 km E of Lusaka, 10 Jan. 1964.) The many essentially parallel "scattered" vascular bundles in a culm are reduced in a rachilla to a few bundles crowded together in the central part of the axis, forming a strand that often appears topographically (but not histologically) like a stele. Branches from this central strand go to the flowers while other branches go to the glumes. The number of branches (traces) going to a single glume depends on how many vasculated veins the glume possesses; often there is only a single trace going to the midvein. In a monopodial rachilla axis, the glume trace(s) leave the central strand at a wide angle below the point where the flower trace(s) leave it that go to the subtended flower. The region along the stem where all these traces leave the central strand and go to one flower and its subtending glume would then be defined as a single node. In a recaulescent sympodial rachilla axis, the glume trace(s) would leave the central strand and would then lie parallel to it in the ground tissue through the next internode before leaving the rachilla to enter the free part of the glume. A cross section of an internode in this case would show the central strand *plus* the one or more glume traces lying around it or on one side of it (Fig. 11d). However, all the sections examined showed only the central strand; at no level were there any other bundles in the ground parenchyma except where, as explained, traces left at a wide angle to go directly to a glume or flower at a node. I must conclude from these preliminary observations that there is no anatomical evidence for recaulescence and therefore sympodiality.

It is true that Arber (1925: 137–148) has shown that in cases of adnation between a stem and a leaf, where the leaf remains a flat lamina and leaflike in its lower part where the stem is adnate, as well as above, the vascular anatomy in the lower part is wholly foliar, there being no trace of a separate stem stele. She gives drawings of *Tilia* (peduncle and bract) and of *Ruscus* and related genera (peduncle and "phyllode," which she interprets as a prophyll bract). One can suppose that the stem bundles in these genera either disappeared in evolution or fused with the midvein of the bract. In our sedge spikelet examples the supposed recaulescent part is stemlike, not foliar, but it is possible of course that recaulescence has really occurred but its anatomical evidence has disappeared because, in this case, the leaf bundles became lost or fused with the stem bundles. But if so, the anatomy would be exactly like that of a monopodial stem so that it cannot be used to distinguish between the two possibilities. When there

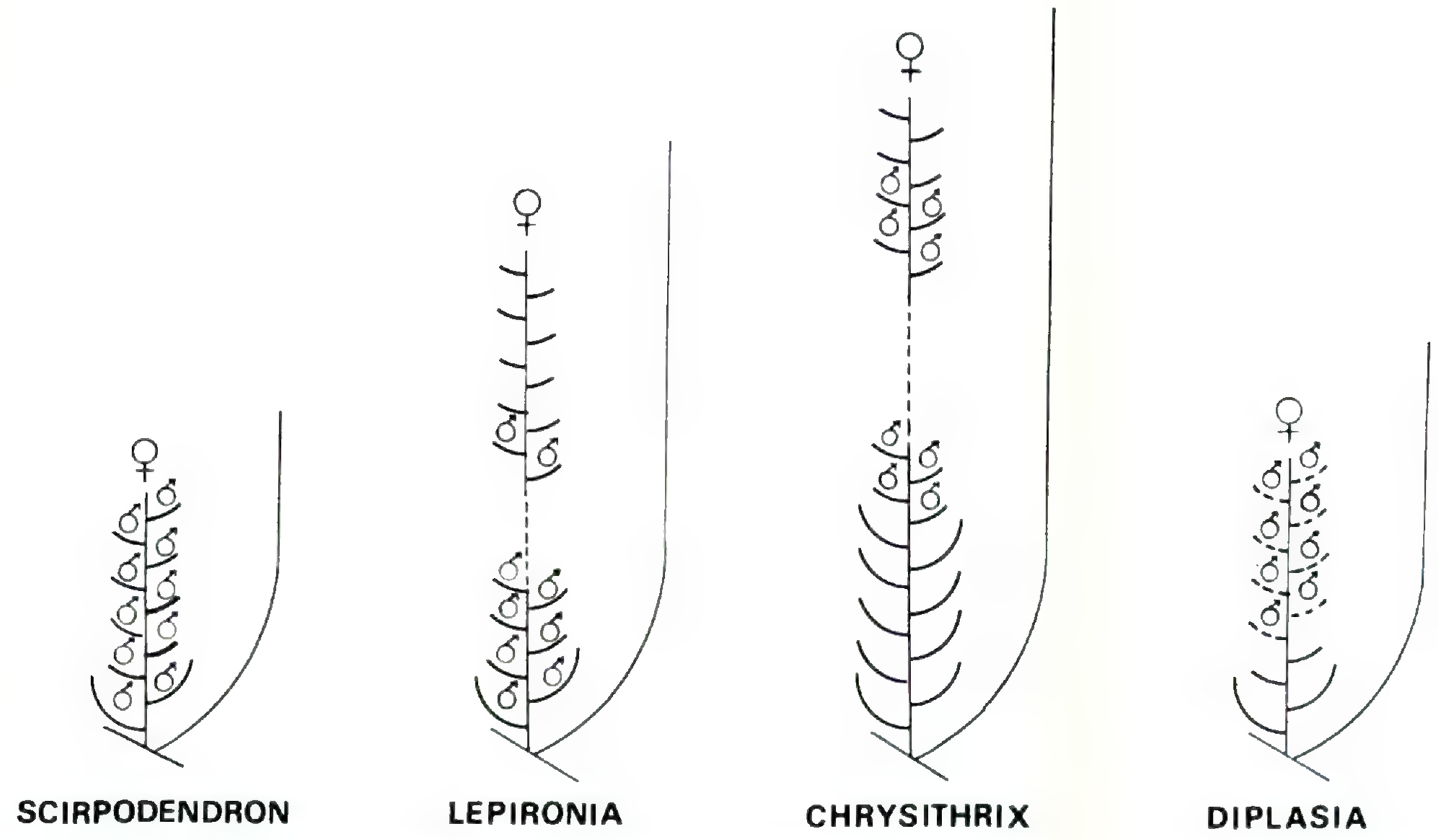


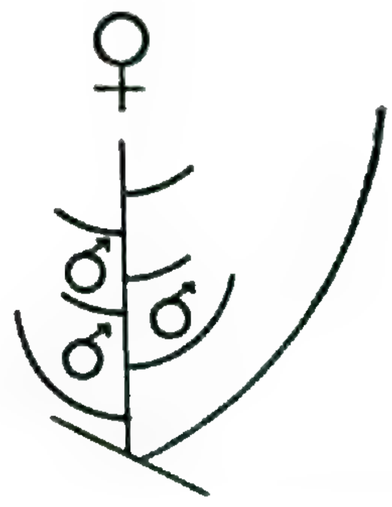
FIGURE 12. Branching patterns of inflorescence units of genera of Group II. The female symbol at the apex of the rachilla represents an apparently terminal female flower of one pistil. The broken-line curves represent glumellas which are supposed to have disappeared in evolution. The broken-line portion of the rachilla represents a continuation of the same arrangement of glumes and flowers. In *Chrysithrix* the basal part of the axis whose tip is the rachilla is the culm (although this is not shown) and is thus similar to *Eleocharis* in this respect.

is no definite evidence that an axis is sympodial, it is morphologically simpler and more logically correct by Occam's Razor to consider it monopodial. (See footnote 5.)

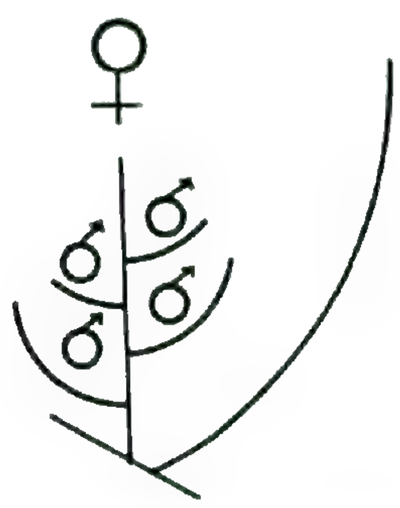
GROUP II

The inflorescence is formed of one or more pseudospikelets. The axis of the pseudospikelet is a continuation of the axis of the culm or of one of its branches of first or higher order. Each pseudospikelet possesses many pseudanthia (a reduced axis with flowers, each looking like a single bisexual flower). Each pseudanthium is hidden by a subtending glumelike covering bract and consists of a very short axis bearing an apparently terminal pistil; beneath this perianthless female flower the axis bears several to many glumellas. A glumella is either empty or bears in its axil a male flower consisting of a single stamen (Figs. 12–13). The two basal glumellas (the most external ones) are always lateral, folded, and have pilose keels. The other glumellas are thinner and glabrous, and are not keeled but flat or slightly curved. In some species of *Hypolytrum*, the two keeled lateral glumellas are the only glumellas present. They may be partially or wholly fused by their margins.

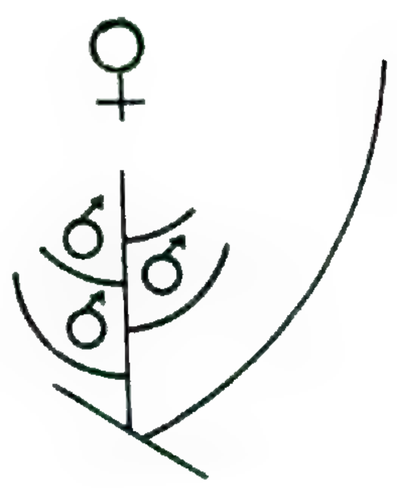
Examples of this group are the following genera, all of the tribe Mapanieae (= Hypolytreae): **Scirpodendron*, **Lepironia* (including *Chorizandra*), *Diplasia*, *Exocarya*, *Mapania*, **Thoracostachyum*, *Mapaniopsis*, and *Hypolytrum*.



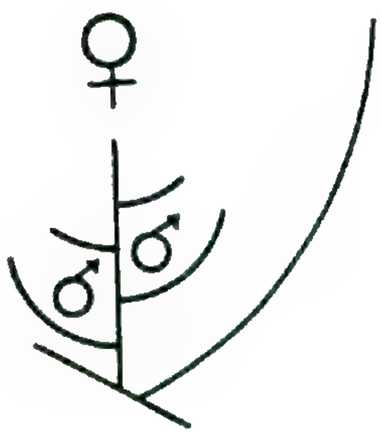
THORACOSTACHYUM
MAPANIA



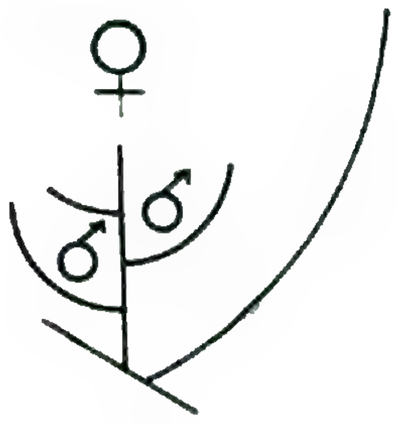
HYPOLYTRUM



EXOCARYA
MAPANIOPSIS



MAPANIA



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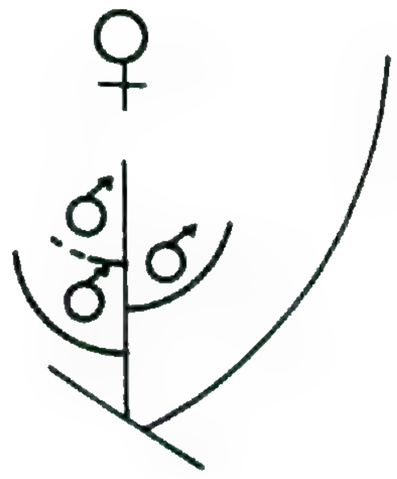

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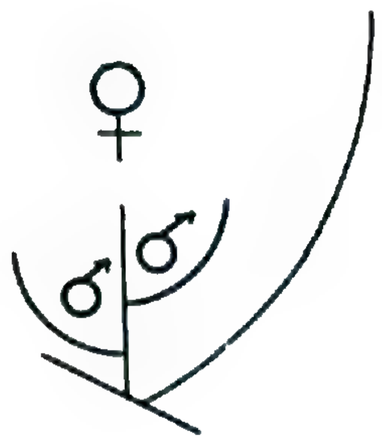

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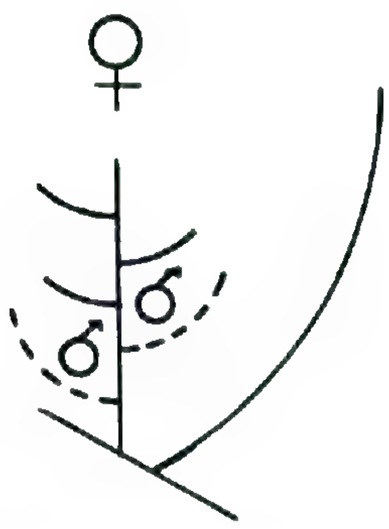
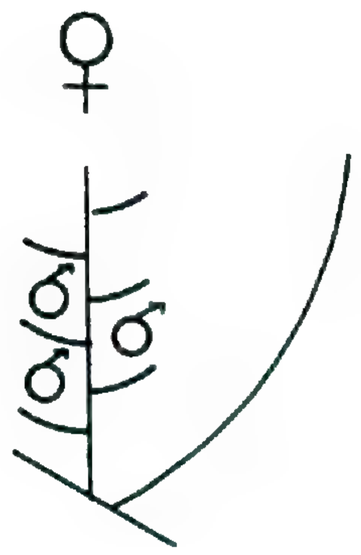


MICROPAPYRUS



SYNTRINEMA

FIGURE 13. Branching patterns of inflorescence units of genera of Group II, showing types of reduction in number of glumellas and flowers. Note that different species of the same genus may be slightly different and that more than one genus may have the same pattern.

Besides these genera which are typical of the Mapanieae, there are three peculiar ones which are also considered to belong to Group II.

The inflorescence of **Chrysithrix* is not made up of pseudospikelets but rather of a single terminal pseudanthium whose axis is the continuation of the axis of the culm; therefore this pseudanthium does not arise in the axil of a subtending covering bract. The glumellas are larger, thicker, glabrous, and not keeled; they could more properly be called glumes. The outer glume extends beyond the pseudanthium and does possess a thick keel at its base. (This outer glume is considered an extension of the culm by some authors, which would then make the axis of the pseudanthium a lateral branch.)

The genus *Micropapyrus*, described in detail in the following article (Eiten, 1976), also forms pseudospikelets but they contain only 1–2 pseudanthia and the glumellas are in the form of bristles. The inflorescence is made up of sympodial branches with wide-spaced pseudospikelets.

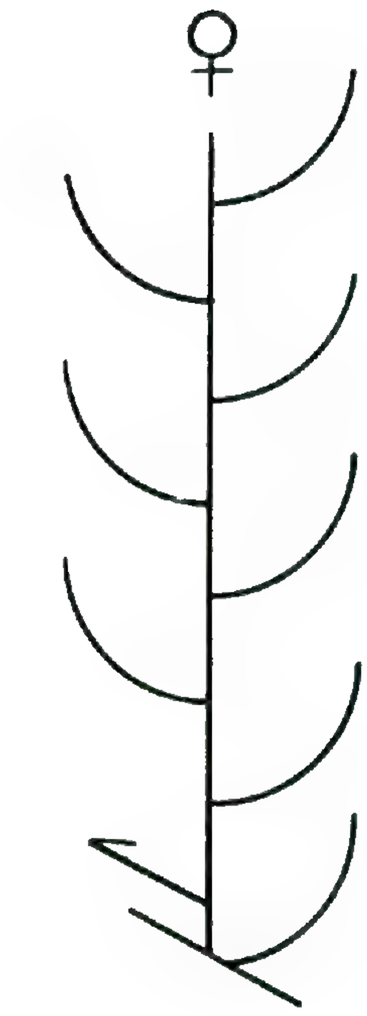
The genus *Syntrinema*, also described in detail in the next article (Eiten, 1976), presents an inflorescence of pseudospikelets united in headlike spikes. The glumellas are free in the lower pseudanthia and are in the form of bristles. The distal pseudanthia in a pseudospikelet are male and do not possess a female flower. The glumella bristles here are lacking or are possibly fused with the filaments which form a column to which are attached the free anthers.

The ultimate inflorescence unit in Group II, then, is of two types: (1) Pseudanthium plus its covering bract. (2) Pseudanthium alone. This is found in only *Chrysithrix*, which has no covering bract.

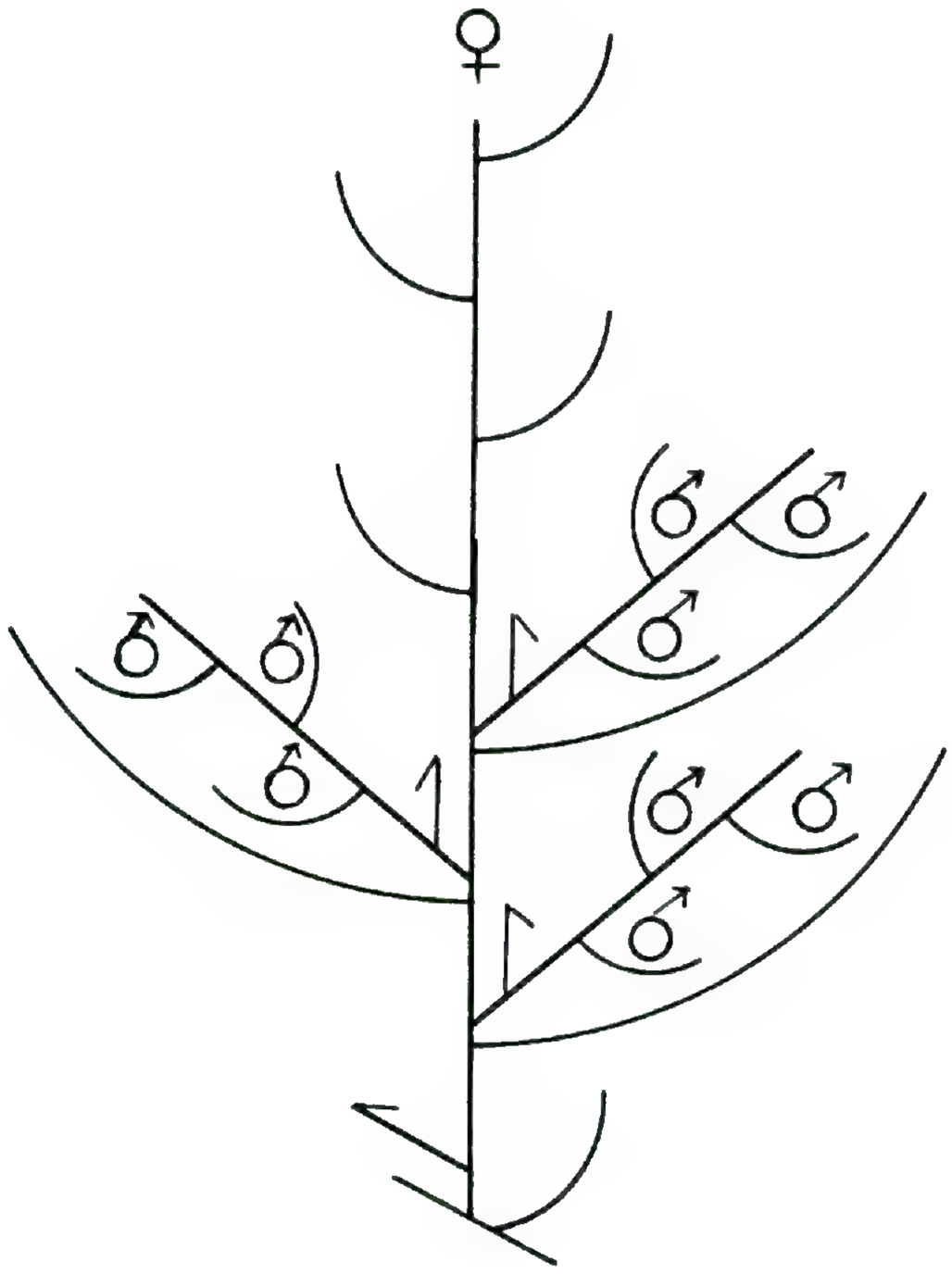
Before taking up Group III, it is necessary to discuss the inflorescence units of the genus *Scirpus*. The interpretation of the bristles of this genus by certain cyperologists, such as Schultze-Motel (1964), has led to the hypothesis that *Scirpus* is derived from the Mapanieae.

In the classical theory, the bristles of *Scirpus* are considered to be a perianth. Since 1888, when Goebel introduced the idea that the "flower" of *Scirpodendron* is an inflorescence, that is, a pseudanthium, this idea was extended to the whole tribe Mapanieae, to which *Scirpodendron* belongs, and afterwards to the tribes Scirpeae, Cypereae, and Rhynchosporeae. According to this theory, what appears to be a simple flower in the genera of Group I is really a reduced inflorescence simulating a true flower. The pistil and each stamen are unisexual flowers. There appears to be a reduction series starting with *Scirpodendron*, *Lepironia* and *Chrysithrix*, passing through *Mapania* and *Hypolytrum* with fewer parts, and arriving at *Scirpus* by way of species such as S. *membranaceus* Thunb. and S. *isolepis* Boeck. In these species, two hypogynous, wide, glabrous scales (supposedly homogolous with the bristles in other species of *Scirpus*) that are lateral in position, folded along the middle but not keeled, are in the same position as the two lateral, keeled glumellas of *Hypolytrum* (see Clarke, 1909: tab. XLVII, 12; tab. XLVIII, 4; tab. LII, 14, 15, 17). Therefore, the floral diagram of these species of *Scirpus* is equal to that of some species of *Hypolytrum* (see Clarke, 1909: tab. CIV, 5, 10; tab. CV, 5, 10, 18; tab. CVI, 7, 12).

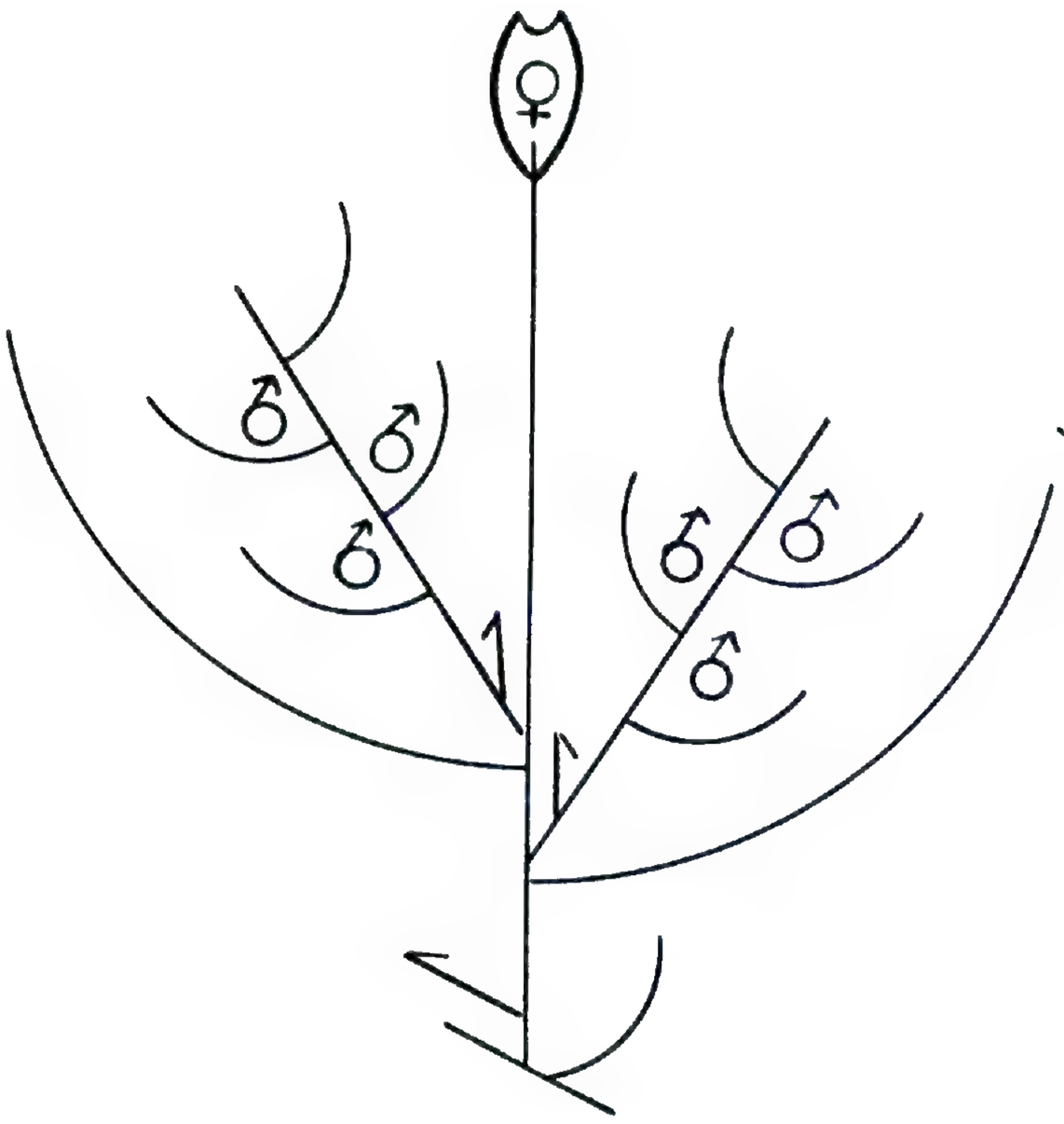
But only this similarity is not sufficient to conclude that *Scirpus* evolved from *Hypolytrum* or from the Mapanieae in general. These two genera are not



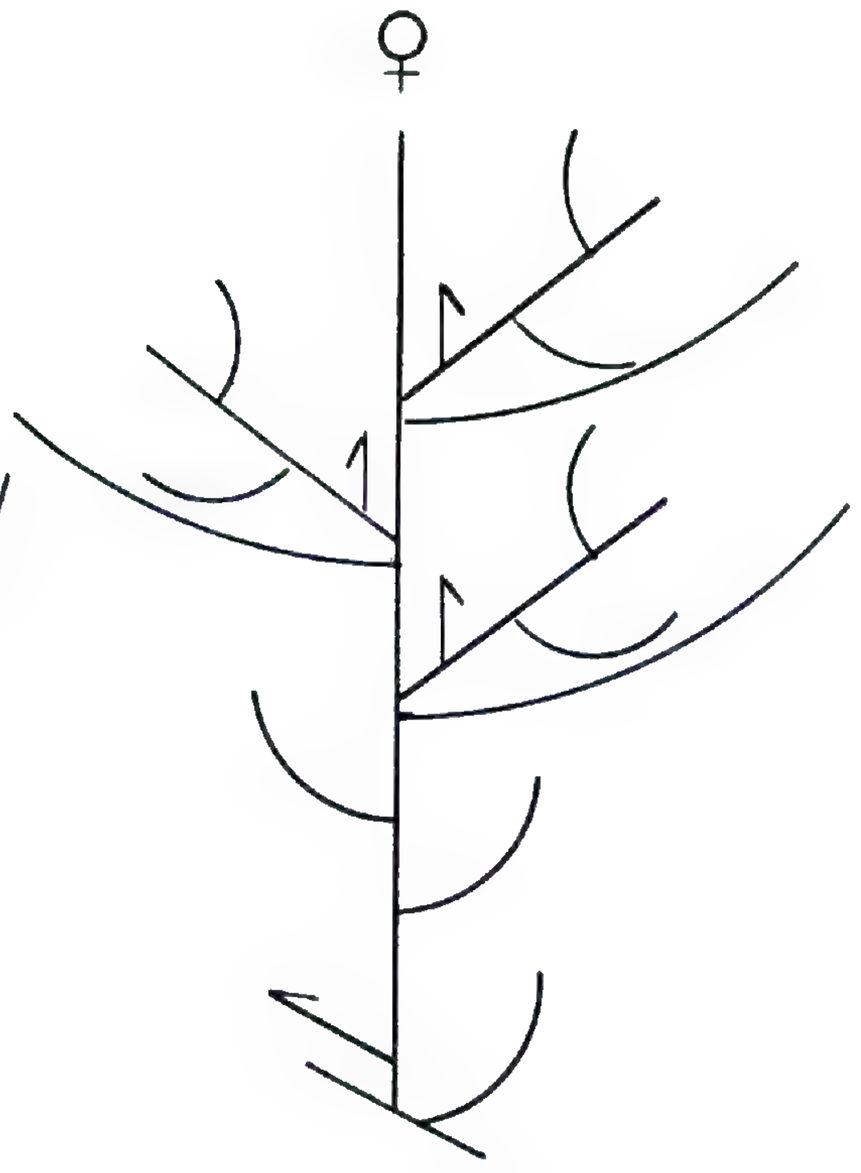
DIPLACRUM



DIPLACRUM



BISBOECKELERA



CALYPTROCARYA

sufficiently similar in other characters to be considered related. The lateral scales of *S. membranaceus* and of *S. isolepis* appear to be a derived form within *Scirpus* and not a primitive form of this organ. (In *Fuirena* and in certain lines in the Compositae, the same thing seems to have occurred: bristles have evolved to laminar structures.) The similarity in the placement of the laminas in these two species of *Scirpus* and in *Hypolytrum* does not indicate a phylogenetic connection but is due to spatial considerations of growth, if it is not merely a coincidence.

It is also necessary to consider *Dulichium* here since Schultze-Motel (1959, 1964) claims that its inflorescence unit is a pseudanthium and its bristles are bracts. He calls attention to the fact that the vascular traces to the bristles on the adaxial side of the pistil separate at a higher level than the traces going to the abaxial bristles which are next to the stamens. The two groups of bristles, as visably separate organs, also separate from the subpistilar axis at different levels. Therefore he claims that the two groups of bristles cannot belong to the same ring and so cannot be calyx parts, and therefore the pistil and stamens cannot be a flower and must be a pseudanthium (synanthium). In the first place, even if the bristles really were bracts, this does not prevent the pistil and stamens from being parts of a single flower because, as is evident from Schultze-Motel's anatomical drawings, the traces of the adaxial bristles arise from different and independent bundles than those from which the stamen traces arise. They do not arise above and from the same bundles as the stamen traces. If they did, this would be an indication that the structure is not a single flower. In the second place, the bristles could well be part of a single ring as is here considered to be the case in *Scirpus*. It is certainly possible that the pressure on the adaxial side of the subpistilar (i.e., floral) axis against the axis (rachilla) from which it sprang caused the base of the adaxial bristles to fuse to the floral axis. If this happened, then, as frequently occurs in flowers, the bundles in the fused parts also fused basally. Schultze-Motel denies this possibility but without any good evidence as far as I can see. When the evidence is not conclusive one way or the other, the most logical thing is to support the simplest hypothesis that the bristles are a perianth ring and the flowerlike structure in *Dulichium* is a true flower. Therefore, the genus belongs in Group I. Since *Dulichium* has characteristics of Cypereae, Scirpeae, and Rhynchosporeae without fitting comfortably in any one, the question is still open as to its tribal position or as to whether it should constitute a separate tribe as Schultze-Motel believes.

Group III

The inflorescence is capituliform but without a central axis or a flat, compound receptacle. The head is composed of branchings of several orders, the whole ex-

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Figure 14. Branching patterns of inflorescence units of genera of Group III. In *Diplacrum*, the inflorescence unit which bears a pistil usually has male-flowered spikelets as lateral branches (right) but sometimes these are absent (left). In *Bisboeckelera* the pistil is contained in an utricle. The branching pattern shown for *Calyptrocarya* represents a specimen seen in which there were no flowers developed in the lateral spikelets. Usually, male flowers of one stamen are borne in the axils of the glumes.

tremely condensed. At the tip of each branch there is an apparently terminal pistil, and below the pistil, there usually occur one or more spikelets of male flowers, the spikelets arising from the same axis that terminates in the pistil. Each male spikelet is subtended by a glumiform covering bract and the rachilla axis just below the spikelet bears a prophyll (Fig. 14).

This group is exemplified by the following genera: *Becquerelia*, *Diplacrum*, *Bisboeckelera*, and *Calyptrocarya*.

In *Becquerelia*, there are usually three male spikelets on an axis (Nees, 1842: tab. 27), but I have seen from 0–7.

In *Calyptrocarya*, I have always seen only three male spikelets (Nees, 1842: tab. 28). In some cases, all three lack stamens (Fig. 14). The empty scales on the axis that ends in a pistil are below the male spikelets.

Diplacrum, as is demonstrated in the following article (Eiten, 1976), possesses a great variability in the pattern of its ultimate branch orders. But the basic pattern is that of Group III. On the axis that apparently terminates in a pistil there are 0–3 male spikelets.

In *Bisboeckelera* (= *Hoppia*) two male spikelets occur below the apparently terminal pistil. The distal empty glumes are fused forming a utricle that encloses the pistil.

The pistil in these genera is *apparently* terminal but may really be only pseudoterminal as Celakovsky (1887) observed.

The ultimate inflorescence unit in this group consists of an axis (rachis) apparently terminating in a pistil, the 0–3 male spikelets (with their adjacent prophylls and subtending bracts) immediately below the pistil, the empty scales (which enclose the pistil) on the rachis just above the male spikelets or in the case of *Calytrocarya*, just below the spikelets. When the prophyll of the rachis and its subtending bract are next to the parts already described (not separated by further branches on the rachis), they too are included in the unit. In complicated cases such as some of the branching patterns shown for *Diplacrum* in the following article (Eiten, 1976), where a rachis with pistil has not only branches which are male spikelets but also other lower branches immediately adjacent, of the same order, and bearing distal pistils, then these female branches (with their prophylls and subtending bracts) are considered to be *separate* ultimate inflorescence units. These lateral female branches may have no male spikelets below their pistil (see Eiten, 1976: figs. 127–128, 130–133, 135 upper branch) or they may have 1–2 male spikelets (see Eiten, 1976: figs. 134, 135 lower branch, 136). In these cases, the unit made up of the original main rachis and its pistil and immediately adjacent male spikelets does not include the prophyll and subtending bract of this main rachis since these are separated from the rest of the unit.

Thus there are two types of ultimate inflorescence units in Group III, those with and those without the immediately adjacent prophyll and subtending bract. In Group III the unit as just defined does not usually make up a visibly distinct unit in the inflorescence head before dissection, but it is unambiguously defined as to what parts it includes.

The genus *Scleria* in classifications of the family is usually placed in the same tribe as *Bequerelia* and *Diplacrum*. In fact, some authors include *Diplacrum* in

Scleria (Koyama, 1961; Kern, 1961; Raymond, 1966). This relationship between *Scleria* and the other two genera has not yet been proved but is only suggested by the similar habit. In the inflorescence of *Scleria* species there are multiflowered spikelets of only male flowers and also spikelets with pistils. The latter have several empty glumes below the pistil and are of three types:

1. Bisexual spikelet (also called androgynous spikelet). At the side of the pistil, there is an apparently terminal axis with glumes subtending developed male flowers (Figs. 15–16, *Scleria virgata* (Nees) Steud., *Schwacke 41830*, Brazil, [RB]). This type of spikelet is also illustrated by Clarke (1909: tab. CXXIV, 3; tab. CXXV, 4) and Robinson (1966) figs. 1–8).

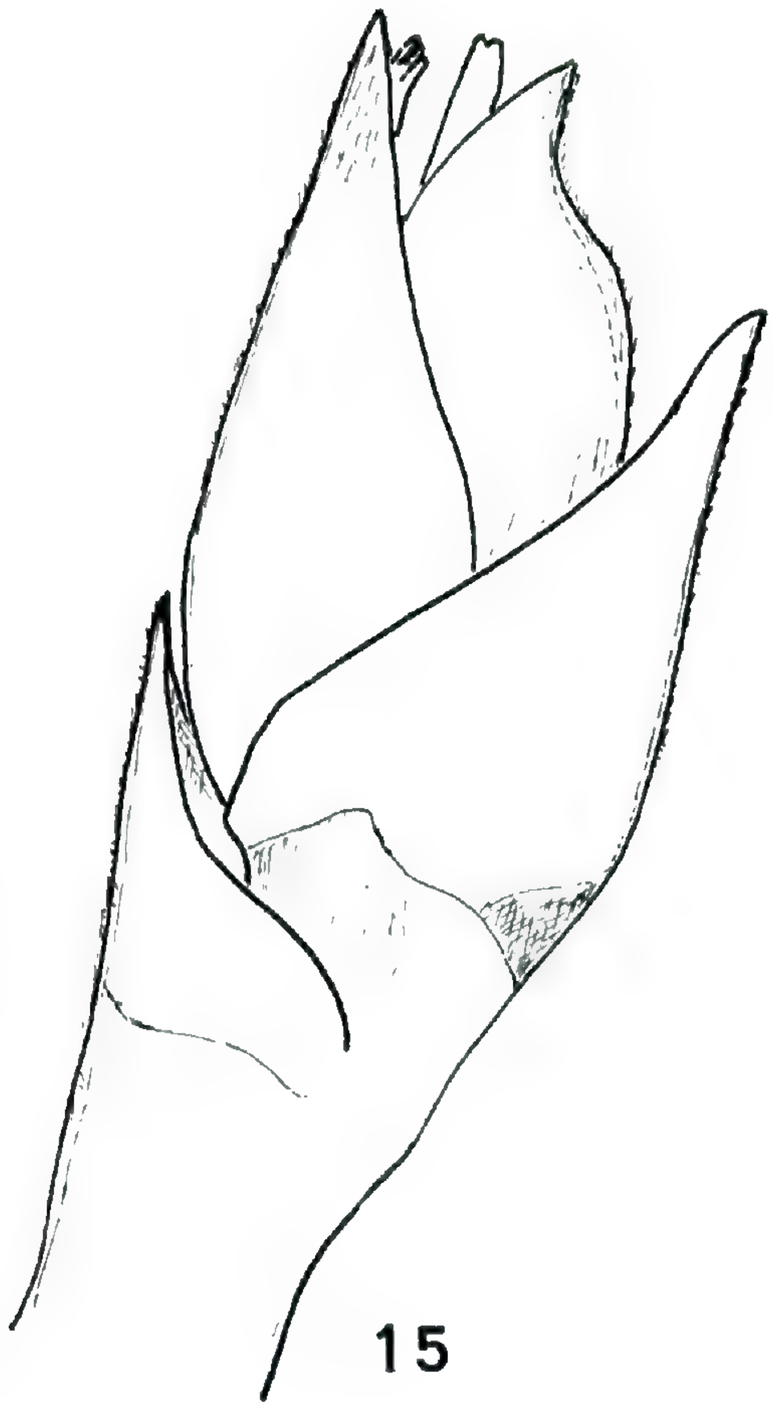
2. Female spikelet with male vestige (also called "subandrogynous"). This structure is similar to the first but the male part is reduced to a few enrolled empty glumellas (Figs. 17–18, *Scleria lacustris* Wright, *Rodrigues & Coelho 1932*, Brazil, Amazonas [INPA]). The same structure, with the vestigial male part even smaller than that shown in Fig. 18, is illustrated by Clarke (1909: tab. CXXVII, 5), by Nees (1842: tab. 26, nos. 19 & 22), and by Robinson (1966: fig. 9, no. 7).

3. Female spikelet. There is no male vestige at the side of the pistil. Illustrations of this type are found in Nees (1842: tab. 22), Clarke (1909: tab. CXXXI, 5), and in Robinson (1966: figs. 11–16).

There are two interpretations of the structure of *Scleria* spikelets which contain pistils. One, held by Nees (1842), Bentham (1883), Holttum (1948), and Koyama (1961), states that the spikelet has only one axis from which arise laterally all the flowers, including the pistillate flower. The male part then corresponds to the distal portion of this axis. The other interpretation, held by Pax (1886), Schultze-Motel (1964), and Koyama (1967, 1969), states that there are two axes in the bisexual spikeletlike structure, one terminating in the pistil and the other, of immediately higher order, arising laterally from the first axis near the base of the pistil and bearing the male flowers.

There is no evidence in the genus Scleria *itself which supports the second interpretation.* At the base of the male part there is no lamina with the form or position of a prophyll which would indicate a new branch. I could find none examining many species of *Scleria*, and Nees (1842), Clarke (1909), and Robinson (1966) do not indicate any in their descriptions and drawings of *Scleria* species. Koyama (1969) illustrated a prophyll at the base of the male part in his branching schemes of *Scleria* in his Figs. 6 and 27. These are based on his Fig. 4, a realistic explosion drawing of *Scleria verticillata*, where he shows a small unmarked scale just above the achene which would correspond to the necessary prophyll. This drawing is obviously redrawn from Fig. 3C of his 1961 paper where this scale does not appear, and where he upholds the lateral position of the female flower.

To justify the terminal position of the pistil, Koyama, in his present view, states that the vascular bundles in the rachilla go in a straight line to the pistil. But in the uniflorous spikelets of *Cyperus* sect. *Kyllinga*, where the flower is undoubtedly lateral, the vascular bundles in the rachilla also go in a straight line to the pistil which appears to be terminal (see Clarke, 1909: tab. I, 3; Kükenthal,



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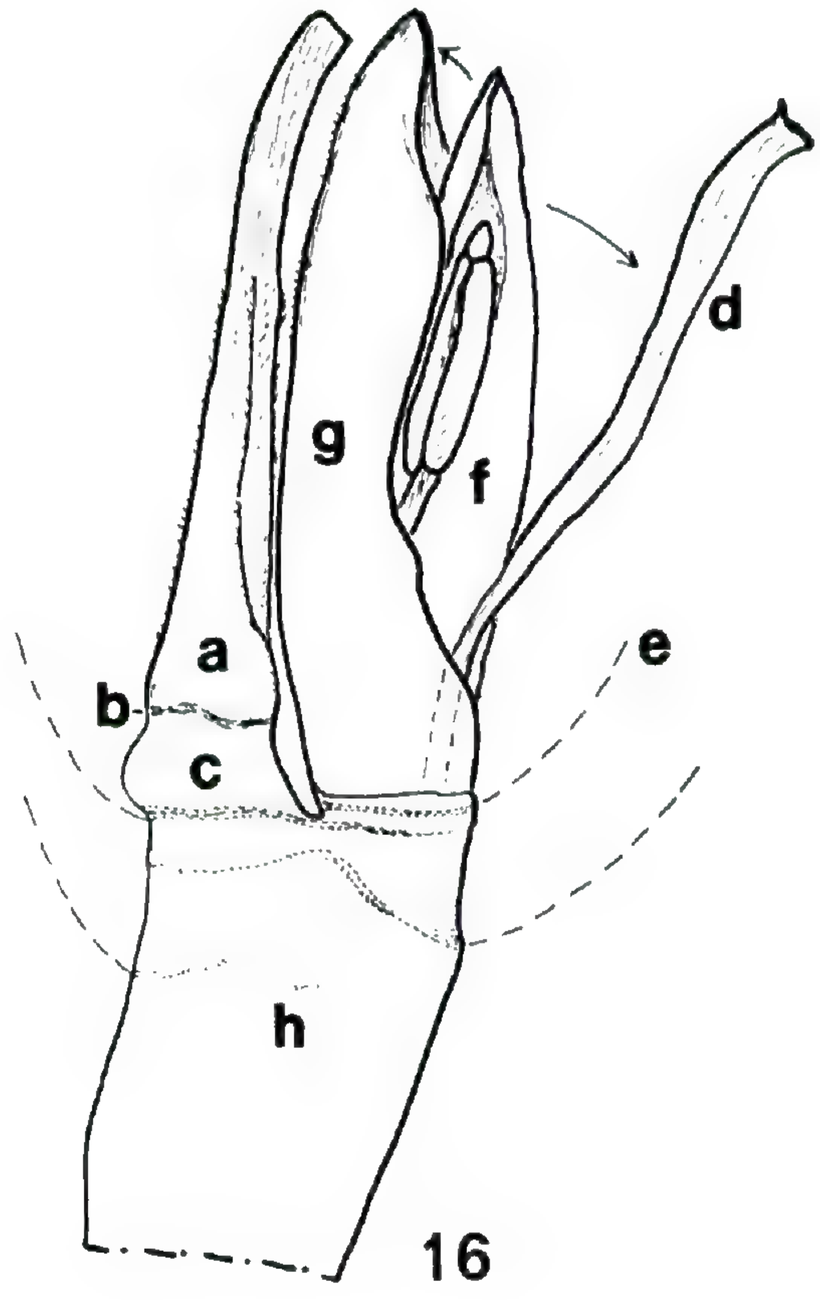

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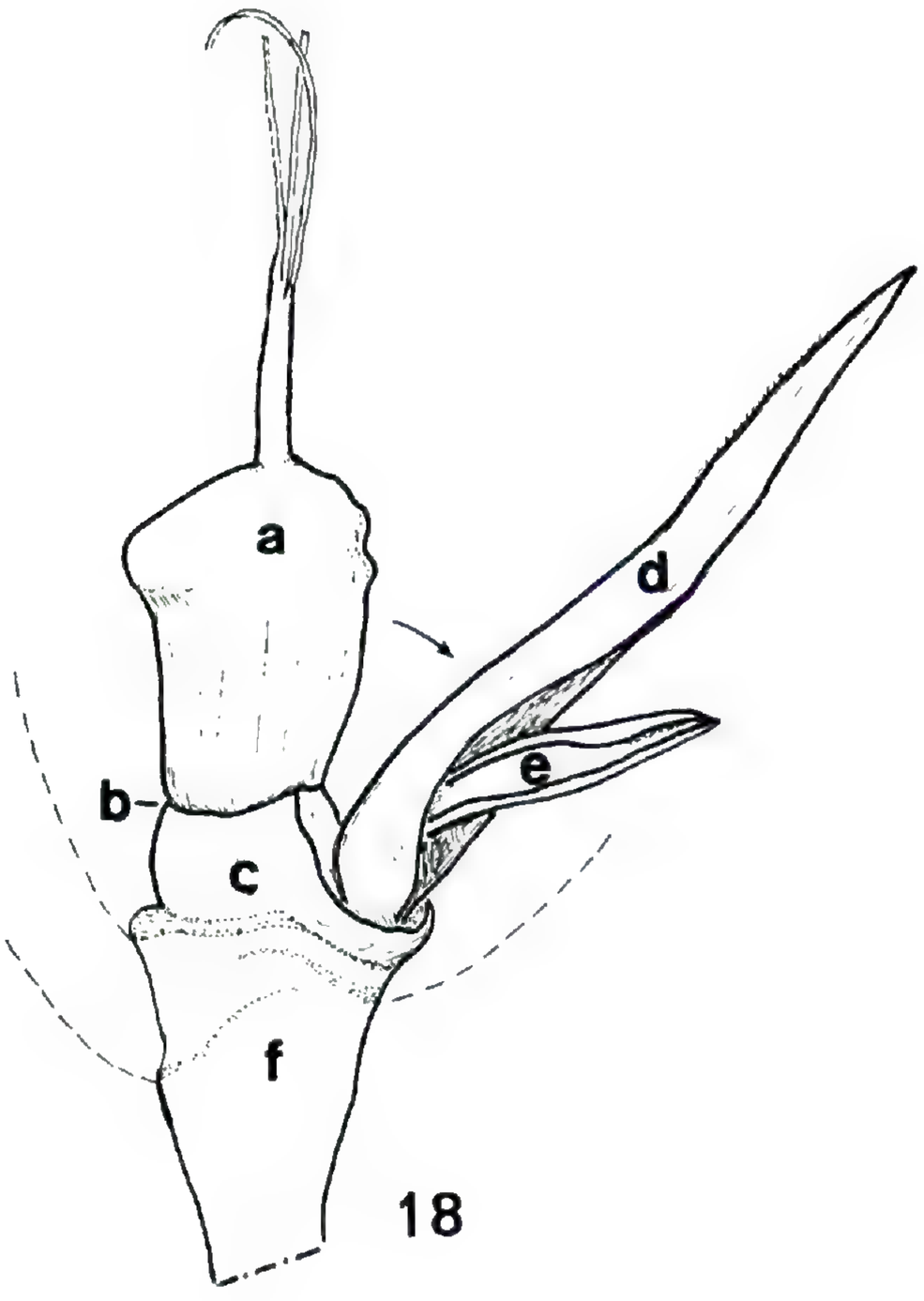

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1935–1936: figs. 62C, 62J, 64H, 64K). Besides this, the distal part of the rachilla bends laterally to continue along the side of the apparently terminal pistil, appearing to be a lateral branch when it really is not. The same thing occurs in *Uncinia* and *Carex*, where the lateral female flower also appears to be terminal (see Kükenthal, 1909: fig. 7C; Mora, 1960: fig. 51; Kukkonen, 1967: fig. 1).

Those who support the interpretation that there are two axes in the bisexual spikelet of *Scleria*, such as Koyama (1969), appeal only to indirect evidence. They maintain, from the general aspect and some other characters, that *Scleria* is related to the four genera cited in Group III, especially to *Becquerelia* and *Diplacrum*. Therefore, by analogy, the continuation of the axis which bears the male flowers in the bisexual spikeletlike structure of *Scleria* would be a new branch as it is in the genera of Group III. In these genera there is usually more than one male spikelet below the pistil. *Scleria*, then, would be a reduction, having only one male spikelet, or none by abortion. But the question is exactly whether *Scleria* really *is* related to the genera of Group III.

I have examined hundreds of collections of *Scleria*, representing species of all the sections of the genus, dissecting the spikelets and making analytical drawings of the branching patterns. I cleared the tissue of spikelet axes (rachillas) to follow the vascular bundles, and also made longitudinal and cross sections. However, the anatomy of mature spikelets does not clarify the problem; it is not possible to know when a vascular bundle forks in the spikelet axis, which branch is the lateral branch, and which branch continues the main axis. (See footnote 5.) Since it was not possible to obtain direct evidence at the level of the "spikelets" (i.e., the ultimate inflorescence units, which contain the last branch orders of the inflorescence), where the internodes and laminar organs are highly reduced, I analyzed the lower branch orders of the inflorescence, recording the branching pattern in diagrams. I noted certain patterns: (1) An axis which bears a pistil may arise from an axis which terminates in a purely male spikelet. (2) An axis which bears a pistil may arise from an axis which also bears a pistil. (3) An axis which terminates in a purely male spikelet may arise from an axis which also terminates in a purely male spikelet. (4) An axis which terminates in a purely male spikelet may arise from an axis which terminates in a bisexual spikeletlike structure, including those with the male part vestigial. (5) An axis which terminates in a bisexual spikeletlike structure may arise from an axis which also

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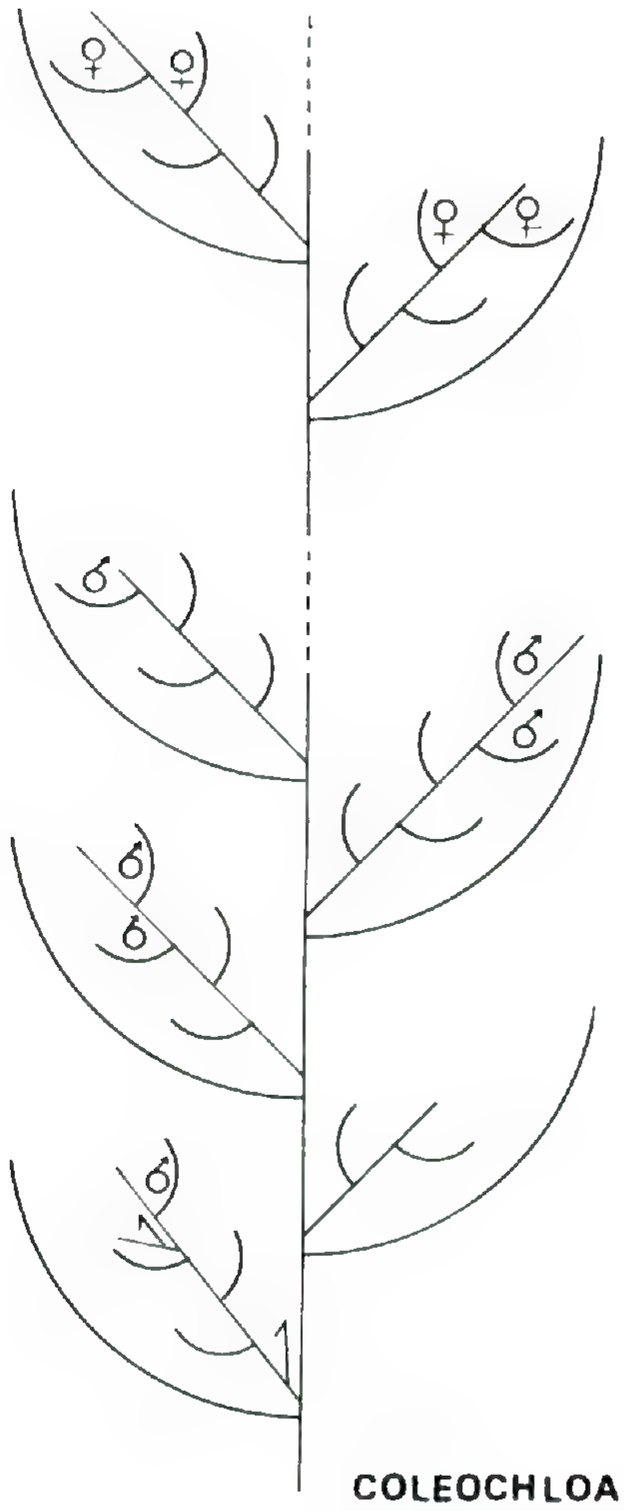
FIGURES 15–18. Aspects of pistil-containing spikelets of *Scleria*; × 8.9—15–16. *Scleria virgata* (Nees) Steud.; *Schwacke 41830*. In this species the male part is well developed and functional. Figure 16 shows the same spikelet as Fig. 15 but with the lower glumes removed (represented by broken lines); a = female flower of one pistil; b = abscision layer of flower; c = axis lateral to the rachilla and which terminally bears the pistil (floral axis); d = filament of lower male flower from which anther has fallen; e = position of glume which subtends lowest male flower; f–g = glumes subtending and enclosing upper male flowers; h = rachilla of spikelet.—17–18. *Scleria lacustris* Wright; *Rodrigues & Coelho 1932*. In this species the male part is vestigial, reduced to two small empty glumes. Figure 18 shows the same spikelet as in Fig. 17 but with the lower glumes removed (represented by broken lines); a = young fruit; b = abscision layer of fruit; c = axis lateral to the rachilla and which terminally bears the pistil (floral axis); d–e = empty glumes of the vestigial male part; f = rachilla of spikelet.

terminates in a bisexual spikeletlike structure. In all five patterns the presence of an evident prophyll indicates an undoubtedly new branch. The only pattern *not* found was an axis terminating in a purely male spikelet arising from an axis which bears a pure female spikelet, that is, one without an associated male vestige. Since this pattern was verified up to the penultimate branch order, it would be strange if it were inverted in the ultimate branch order. Therefore, in the bisexual spikeletlike structure, the male part would not seem to be a new branch which arises from an axis which terminally bears a pistil. These observations furnish direct evidence from the genus *Scleria* itself that the pistil in a bisexual spikeletlike structure is lateral, that is, that there is only one axis and so the structure is a true spikelet. This conclusion is strengthened by observations on *Scleria bracteata* Cav. and S. *cyperina* Kunth. In both, the pistillate spikelets are always on the basal branches of the inflorescence (Nees, 1842: tab. 24), that is, there is a tendency in the genus for the female part to be basal in relation to the male part. Mora (1960) also noticed this tendency in *Scleria*. There is another tendency within the family which supports the lateral interpretation of the female flower in *Scleria*. In genera in which there are true spikelets with all the flowers lateral and almost always bisexual, such as *Cyperus* and *Eleocharis*, when there is a reduction in the sexual parts, it is almost always the pistil which aborts, producing a male flower. When this happens, it always ocurs in flowers in the upper part of the spikelet, the basal flowers remaining bisexual.

As to the supposed relation between *Scleria* on the one hand and *Bequerelia* and *Diplacrum* on the other, it is interesting to note that the typical branching pattern of the inflorescence of the two latter genera is one in which axes which terminate in male spikelets arise from axes which apparently terminate in pistils, exactly the only pattern which does not occur in *Scleria*.

The bisexual spikelet in *Scleria* is similar in its branching pattern to that of *Rhynchospora* (Fig. 1). However, I do not include *Scleria*, which always has unisexual flowers, in Group I because, characteristically, the flowers in the genera of this group are bisexual. (In the Rhynchosporeae some but not all the flowers in a spikelet are male.) Although *Scleria* is similar to *Schoenoxiphium* and *Kobresia* in branching pattern and sex of flowers, I do not include it in Group VI because the female flower is not inside a utricular or semiutricular prophyll. Not being able to place *Scleria* in any of the six groups presented and not having irrefutable evidence as to what the structure of its ultimate inflorescence unit really is, I prefer to leave the position of the genus to be decided on the basis of future studies.

Since *Scleria* does not seem to have the same structure as the four genera of Group III, it cannot be combined with them in the same tribe. These four genera are distinct enough to be in a tribe of their own. The oldest name at a tribal level is Hoppieae Pax, 1886, based on the illegitimate *Hoppia* Nees, 1842, a later homonym of *Hoppia* Spreng., 1818 (Gentianaceae, = *Hoppea* Willd., 1801). Pax's Hoppieae, however, also included his subtribe Chrysitrichinae, i.e., the present tribe Mapanieae, so that my Group III really corresponds to Pax's subtribe Hoppiinae. However, since a tribal name must be based on a legitimate generic name, the present tribe must then be called Bisboeckelereae Mattf. in Diels, 1936.



COLEOCHLOA

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TRILEPIS

TRILEPIS

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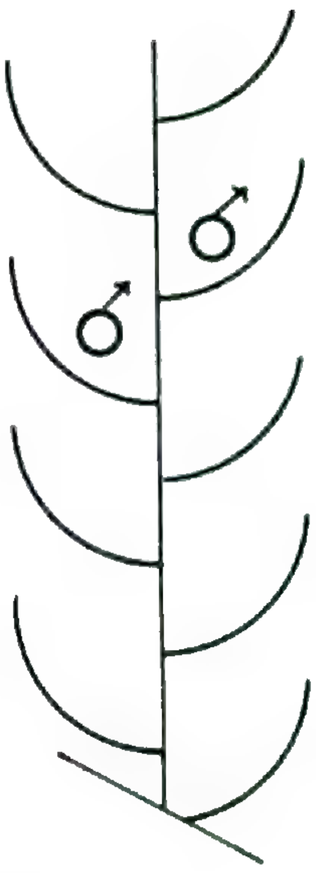
FIGURES 19–20. Branching patterns of "compound spikelets," inflorescence units of genera of Group IV.—19. *Coleochloa*. This particular example is of an exceptional specimen in which the female true spikelets bear two female flowers, which are therefore lateral, instead of the usual one which is pseudoterminal, although generally considered terminal.—20. *Trilepis*. Left, male compound spikelet; right, female compound spikelet.

GROUP IV

The inflorescence is formed of "compound spikelets." These are the ultimate inflorescence units which can be externally delimited visually and resemble from the outside the true spikelets of Group I. The compound spikelet is composed of an axis which laterally bears few to many unisexual true spikelets (the "partial spikelets" of Koyama & Maguire, 1965). Each true spikelet arises in the axil of a glumiform covering bract; its rachilla bears one or more lateral flowers subtended by glumellas. Sometimes a prophyll is visible at the base. The "compound spikelet" is, then, really a panicle. It is unisexual in *Trilepis*, that is, all the true spikelets in the "compound spikelet" have flowers of the same sex (Fig. 20); in the inflorescence, the male compound spikelets are in the lower part and the female ones in the upper part. In **Coleochloa* the compound spikelet is bisexual, that is, the true spikelets at the base of the compound spikelet are male, while the true spikelets in the upper part of the compound spikelet are female (Fig. 19). Some of the true spikelets, at the apex or the base of the compound spikelet, have no flowers.



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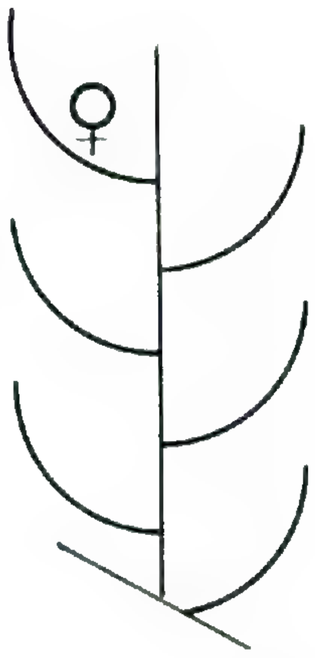

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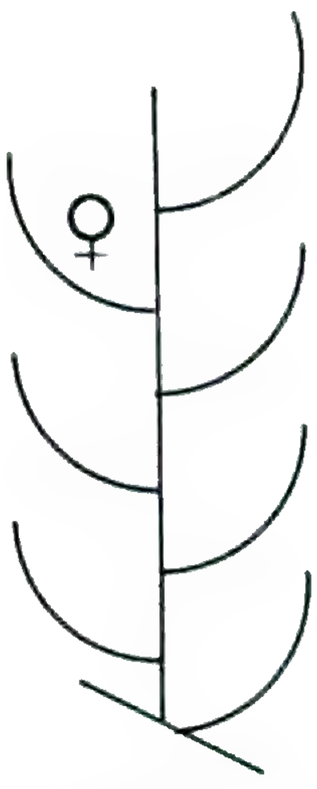
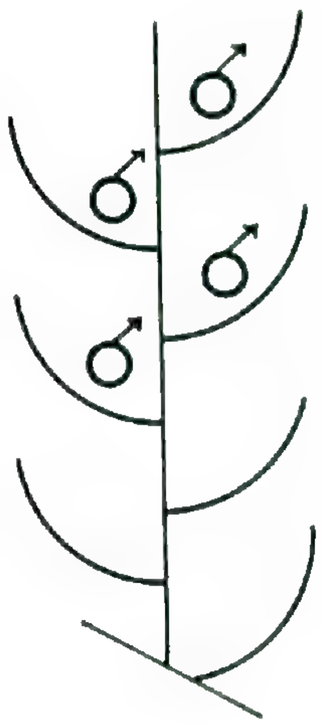
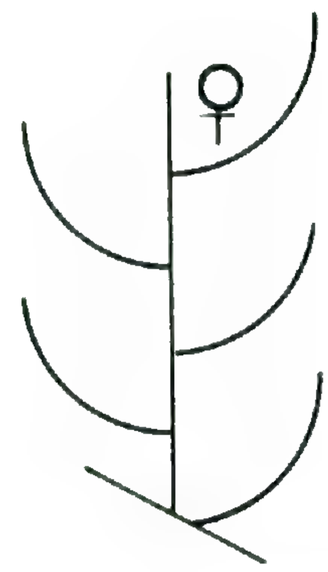


EVERARDIA



EXOCHOGYNE



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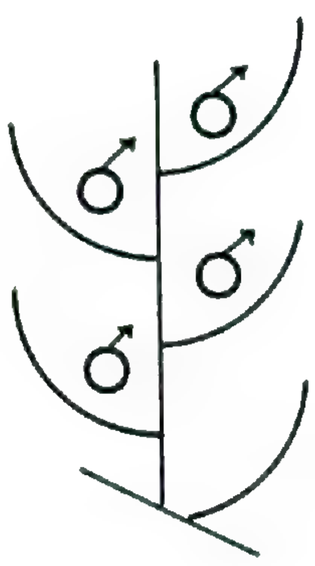
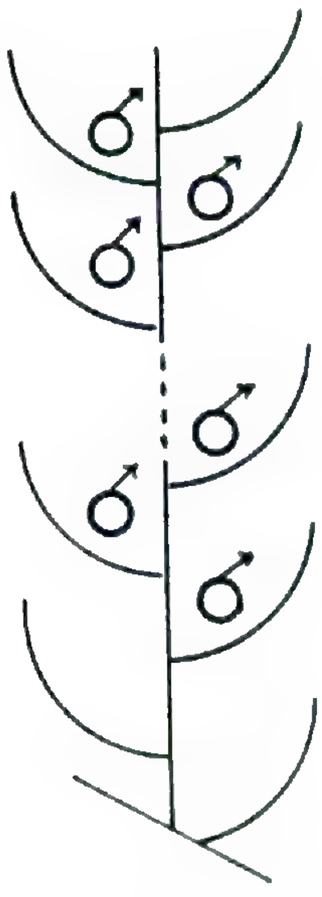


LAGENOCARPUS



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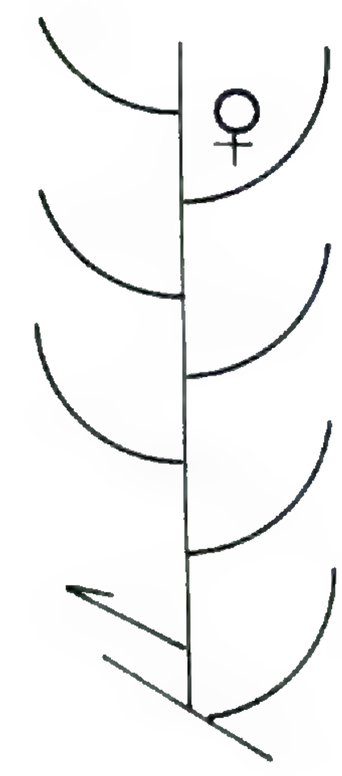

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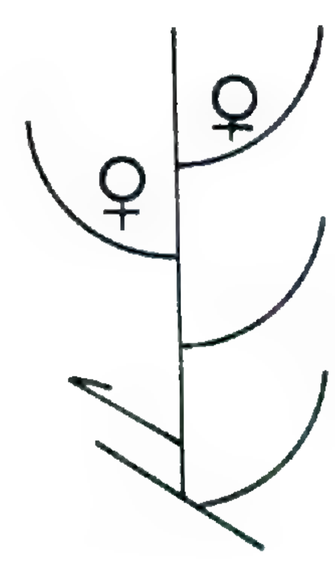

LAGENOCARPUS

The ultimate inflorescence unit in this group is of two types: (1) "Compound spikelet" with the prophyll and subtending bract of its main axis if these laminas are immediately adjacent. (2) "Compound spikelet" without these laminas if they are not immediately adjacent but separated by other branches on that axis.

Two genera exemplify this group: **Coleochloa* and *Trilepis*.

Group IV contains those genera of the tribe Lagenocarpeae with "compound spikelets." Besides *Coleochloa* and *Trilepis*, it also includes the African genera, *Afrotrilepis* and *Microdracoides*. The female flowers of all the genera of this tribe are considered truly terminal by Pax (1886), Schultze-Motel (1964), Koyama & Maguire (1965), and Koyama (1969), but there exists evidence contrary to this view. The female spikelet is always described as having empty basal glumes and the terminal pistil as being enveloped in the most distal glume. But possibly the pistil arises in the axil of this distal glume and is therefore lateral, that is, "pseudoterminal." By the simple outward appearance one cannot distinguish between these two possibilities.

Examining a collection of *Coleochloa setifera* (Ridley) Gilly from Tanzania, Africa (*Richards 20007*, duplicate examined in my personal herbarium, other duplicate in K), I found that all its female true spikelets had *two* pistils at the apex of the rachilla, at almost the same level, both well developed and each subtended by a glume (Figs. 19, 36–37). Two pistils cannot both terminate the same axis. In some "compound spikelets" the upper female flower had no further organs above it, so the branching pattern would be like that shown in Fig. 19. In other "compound spikelets" there was a glume above the upper female flower, as shown in Fig. 36. The latter case is particularly strong evidence that both female flowers are lateral on the rachilla. Therefore, in this genus, even when there is one pistil, as from the literature there usually seems to be, it is lateral.

Group V

The inflorescence terminates in spikelets which are isolated or grouped in fascicles. These are true spikelets. The male spikelets possess basal empty glumes and few to many distal lateral staminate flowers. The female spikelets have several basal glumes and what is usually considered a terminal pistil (Fig. 21).

This group is exemplified by: *Lagenocarpus* (including *Cryptangium*), *Cephalocarpus*, **Everardia*, **Didymiandrum*, and **Exochogyne*.

The genera of this group are those of the tribe Lagenocarpeae which do not have "compound spikelets" but only true spikelets.

The ultimate inflorescence unit in this group is the male or female spikelet plus the prophyll (when present) and subtending bract of the rachilla axis.

The branching pattern of the ultimate inflorescence units of this group differs from that of Group I only if the pistil really is terminal, which is the general

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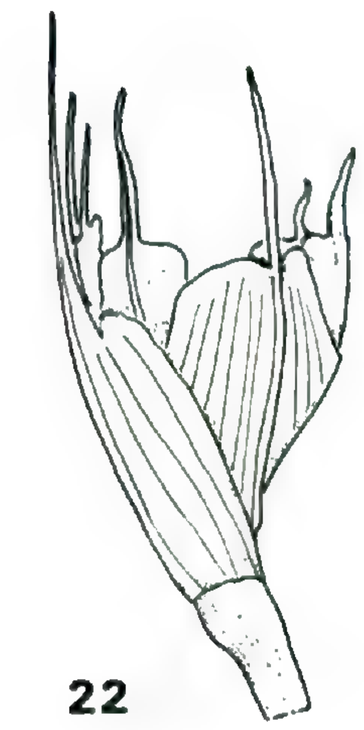
Figure 21. Branching patterns of inflorescence units of genera of Group V. Note variation in number of glumes and flowers in the same genus and that the prophyll is not always present. In Figs. 19–21 the apical pistil is shown as a lateral (pseudoterminal) female flower, in accord with the position adopted in this paper, rather than as a terminal flower.



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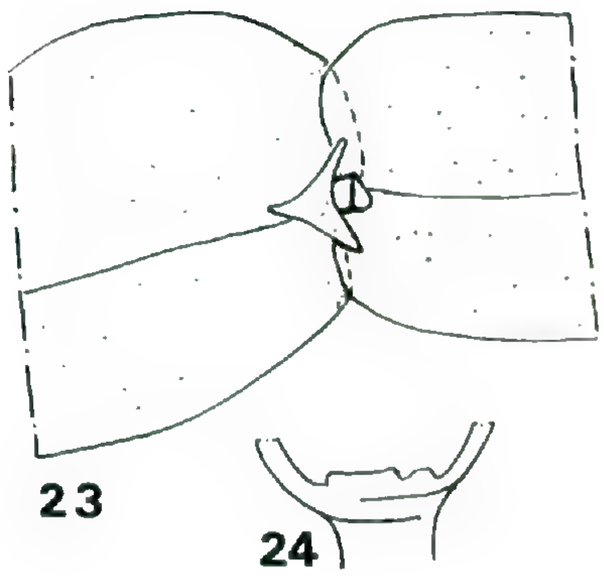

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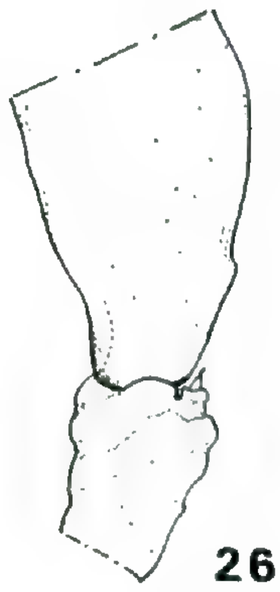

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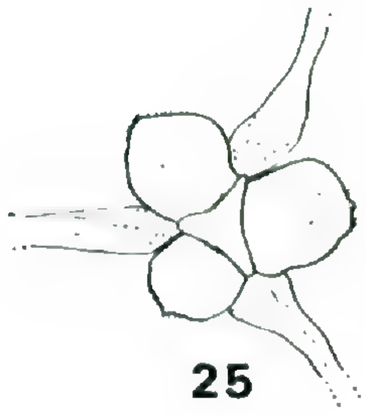

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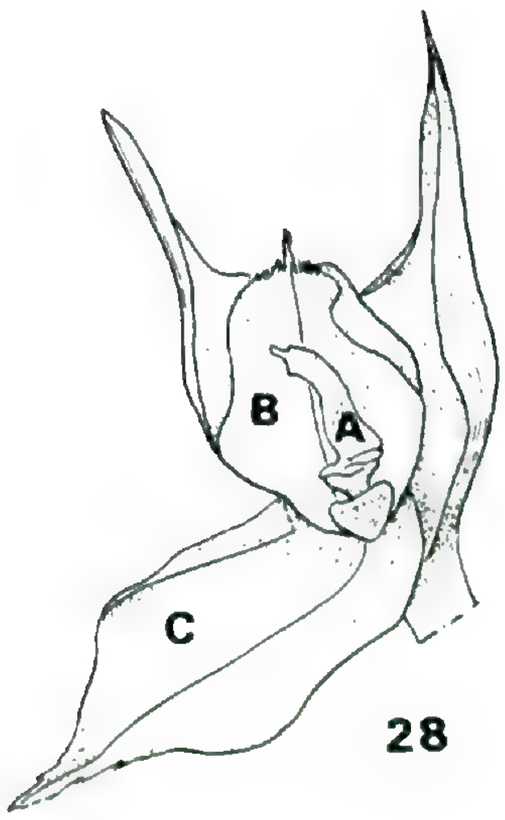

B A C

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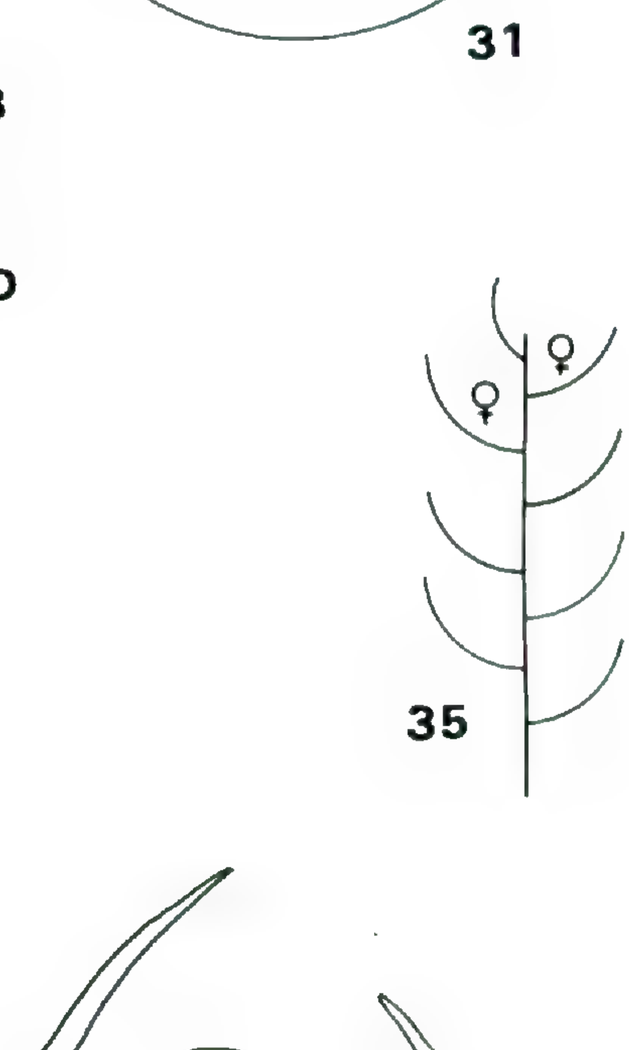

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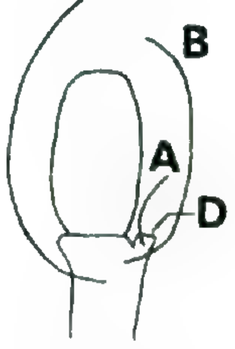

B A D

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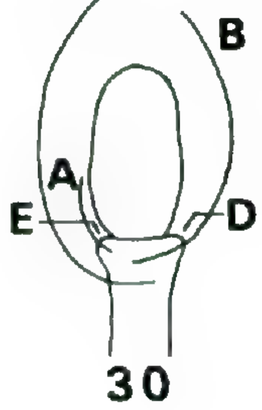

C B A E D

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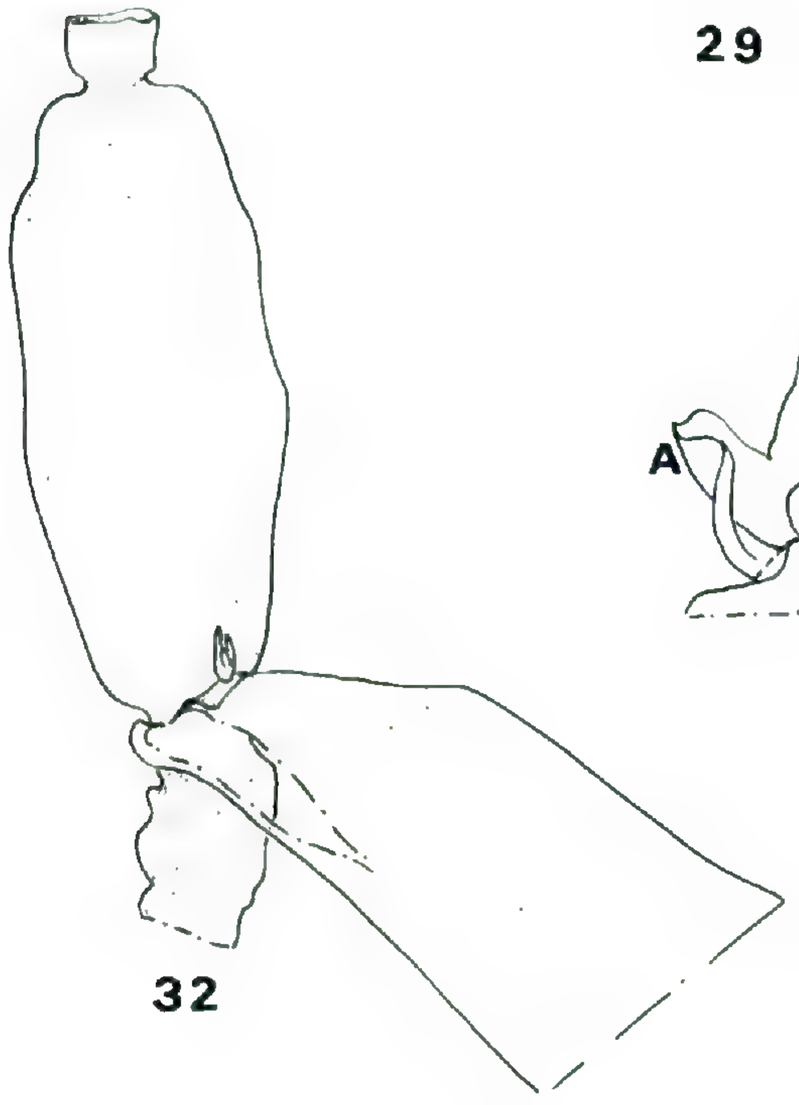

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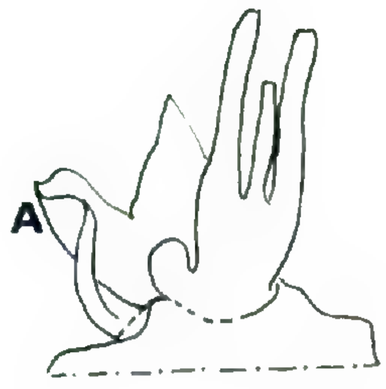

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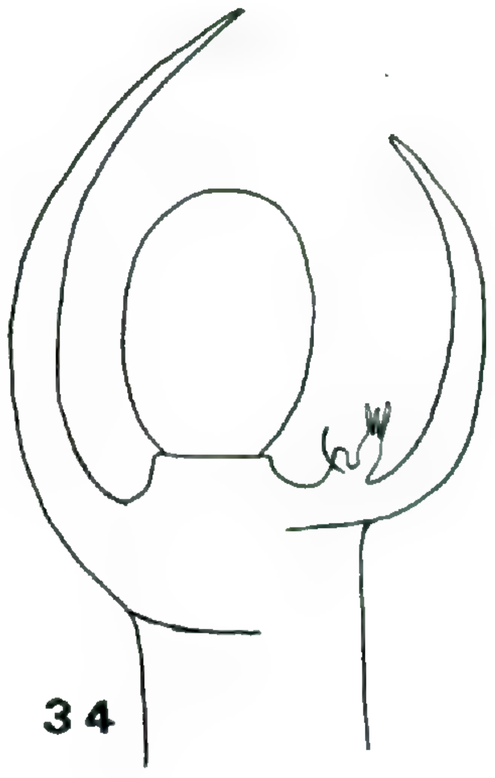

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opinion of cyperologists. But there is doubt in this respect. Observations I have made show that the female flower is really lateral. In a collection of *Everardia surinamensis* Gilly, (*Maguire et al. 53714*, Venezuela, det. Koyama, duplicate in UB examined, other duplicates occur in NY and other herbaria), the pistil at the apex of the female spikelet was observed to be subtended by the penultimate distal glume. The rachilla continued beyond the base of the fruit, bearing a well reduced ultimate glume. The pistil in this collection, then, was clearly lateral in the axil of the penultimate glume.

A similar series of observations was made in *Lagenocarpus rigidus* Nees (subsp. *rigidus*, *Irwin et al. 12995*, Brazil, near Brasília, det. Koyama, [UB]; subsp. *tenuifolia* (Boeck.) Koyama & Maguire, *Brade 13522*, Brazil, Minas Gerais, Diamantina, det. Koyama, [RB]). Several constructions were noted at the apex of the female spikelets. They all have several large glumes below an apparently terminal female flower or fruit (Fig. 22). However, careful examination of the rachilla tip

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FIGURES 22–35. Views of parts of female spikelets of *Lagenocarpus rigidus* Nees.—22. Cupule of glumes of a female spikelet, the mature fruit having been pulled out; *Brade 13522*; × 6.5—23. View of base of the interior of this cupule showing the penultimate glume on left, ultimate (most distal) glume on right, the raised triangular scar left by the fruit, at its right a depressed rectangular area representing part of the distal surface of the rachilla, and at its right a small triangular area of raised tissue representing the apex of the rachilla; × 18.—24. Diagram showing profile of the surface shown in Fig. 23.—25. View of base of the fruit which was pulled out of this cupule of glumes, showing scar, 3 grooves, and 3 hypogynous squamellae. —26–27. Distal part of rachilla and base of fruit showing, respectively, side and dorsal views of rachilla apex at the side of the base of the fruit; *Irwin et al. 12995*; × 22. In Fig. 27 the thin extension to the left from the parenchymatous rachilla point represents a very small vestigial glume.—28. Cupule of glumes with lower glumes and fruit removed and front (penultimate large) glume, C, pulled down to show fruit scar and vestigial glume, A; × 6. The vestigial glume is wrinkled in its basal portion and has been pressed by the fruit against the ultimate large glume, B. (A single short length of vein, not demarked here, occurs on the right side of the vestigial glume about midway between its base and tip.)—29. Diagram interpreting the two possibilities of the construction shown in Fig. 28. See text for discussion.—30. Diagram showing possible interpretations in the hypothetical case of the vestigial glume, A, being on the opposite side of the fruit from the ultimate large glume, B. This construction was *not* seen in the material examined. Here, there would be three indistinguishable possibilities: (1) The fruit is in the axil of the ultimate large glume, B, and the apex of the rachilla is on the opposite side at E. (2) The fruit is in the axil of the vestigial glume, A, and the apex of the rachilla is on the opposite side at D. (3) The fruit is terminal.—31. Cross-sectional diagram of a female spikelet examined (that shown in Fig. 22) showing fruit scar, position of rachilla apex (dark spot next to scar) and the glumes. The absolute size of the glumes is not indicated but the position of the midvein of each and the proportion of the circle it covers near its base is accurately shown. This spikelet was representative in its phyllotaxy of several examined.—32. Distal portion of rachilla, ultimate large glume (torn at base) and fruit of a female spikelet. The other glumes were removed. At the base of the fruit can be seen a vestigial pistil (shown magnified in the following figure); *Irwin et al. 12995*; × 22.—33. Vestigial pistil of Fig. 32, showing the three styles, and on its left side a small spherical projection of tissue which is the apex of the rachilla; × 56. Back of the pistil is a vestigial glume (its base torn from its connection around the front of the pistil and pushed back). Its single vein is along its fold at A. It is not clear whether the large notch at the far side of the glume is natural or a result of tearing during preparation. —34. Diagram showing placement of the organs at the distal end of the rachilla of the female spikelet of Fig. 32.—35. Branching pattern of this complete spikelet, showing the number of glumes actually found in it. Since the axis of this spikelet bore other organs below, its prophyll and subtending bract were not next to the spikelet.

FIGURES 36–37. True spikelets of *Coleochloa setifera* (Ridley) Gilly with two female flowers each; *Richards 20007*; × 13.5.—36. The subtending bract of the true spikelet is shown, partially detached, at right, the two lower empty glumes, and the two upper glumes, each with a pistil.—37. In this spikelet, the subtending bract is not shown and the pistils are at an earlier stage of maturity. The lower pistil is covered by its glume but the long ovary hairs are visible.

around the base of the fruit showed a small raised point of tissue that is the apex of the rachilla (Figs. 23–24), or the apex with a projection interpreted as a vestigial glume (Figs. 26–27). In both cases the fruit appeared to be in the axil of the *penultimate* large glume; this is particularly evident in Fig. 23. When the raised point is the rachilla apex alone, the branching pattern would be as in Fig. 21, bottom row, middle. It should be emphasized that the small bits of tissue referred to are *not* the hypogynous squamellae at the base of the fruit. Figure 25 shows a basal view of the fruit that was pulled out of the cupule of glumes whose inside is shown in Fig. 23. All the squamellae went with the fruit but the raised bit of tissue referred to is still in the cupule and separate from the scar left by the fruit (Figs. 23–24). In another case the raised rachilla apex grew concrescent to the base of the ultimate large glume, appearing as an outgrowth on its base rather than separate as in the previous case.

Another construction is shown in Fig. 28. Here, a much better-developed vestigial glume, A, arises from the rachilla tip on the *same* side of the fruit as the next lower and larger glume, B. The central axis of both the vestigial and the adjacent large glume are on neighboring radii. This can only be interpreted as in Fig. 29, and it allows two possibilities: (1) The fruit is lateral and in the axil of the penultimate large glume, C. (2) The fruit is terminal on the thick rachilla and glumes B and A are borne on a new side branch (D) arising from that rachilla just below the fruit. The latter interpretation is similar to Koyama's present view of *Scleria*. As in *Scleria*, there is no direct evidence for the existence of a new branch since the vestigial glume does not have the aspect of a prophyll. Since the latter interpretation is the more complicated of the two, it should not be accepted without further evidence. The simpler interpretation that the axis is unbranched and the fruit is lateral is preferred. For if the fruit were terminal on an unbranched rachilla, then the vestigial glume (when there is one) would have to be on or near to the *opposite* side of the fruit from the uppermost large glume, such as is represented in Fig. 30. This is because the phyllotaxy of the glumes in a female spikelet, although not regular, is such that successive glumes are not

next to each other (that is, on radii forming small acute angles) but are on radii about 100°–180° apart (Fig. 31). The vestigial glume being on the side of the fruit opposite from the uppermost large glume is a necessary, but not the sole, condition for the fruit to be interpreted as terminal, for two other interpretations are also consonent with this position, namely, that the fruit is lateral and in the axil of the uppermost large glume, or, less likely, that the fruit is lateral and in the axil of the vestigial glume.

In another case, two vestigial glumes around a raised rachilla apex at the side of the base of the fruit was observed.

Another and rarer construction is the presence of a second and more distal pistil at the rachilla tip. This was noted several times. In one case the second pistil was relatively large but no other part was noted distally to it. In this case the interpretation of the spikelet would be like that indicated in Fig. 21, bottom row, right, that is, both pistils are lateral on the same axis. It is true that one could argue that the lower pistil is terminal on the main rachilla and the second pistil terminal on a side branch even though there is no independent evidence for such a branch. But this argument would not hold for the case illustrated in Figs. 32–34. Here, besides the vestigial second pistil in the axil of the ultimate large glume (the lower pistil, now a fruit, being in the axil of the penultimate large glume), there is a vestigial glume distal to the vestigial pistil, as well as a clearly visible rachilla apex. This arrangement certainly shows that the second pistil is lateral. Therefore, unless one is prepared to argue that the first pistil is terminal and the second is lateral, a very complicated hypothesis for which there is no independent evidence and which is contrary to all rules of morphology in the Cyperaceae, one must recognize that both pistils are lateral on a single axis, as diagrammed in Fig. 35.

The genera of Group V have not been placed in Group I because the lateral nature of the pistil has not yet been proved for all its genera but mostly because the flowers are all unisexual.

The evidence that in certain collections in several genera of the Lagenocarpeae the female flower is lateral, as well as the probable lateral nature of the female flower in *Scleria*, shows up a certain weakness in Koyama's definition of the subfamily Mapanioideae (1967, 1969, 1971)[4] defined as having terminal female

[4] Koyama calls the fruit in this subfamily a "fructification" because it consists of more than the mature ovary. However, there is no necessity for a new term. In other families of the angiosperms a fruitlike structure incorporating other parts besides the mature ovary has always been called a "simple accessory fruit." He calls the external tissue surrounding the pericarp a "utricle." This term is not well chosen since utricle means "bladder," that is, a structure which is inflated, with a rather large space around what it surrounds and with the outer wall rather soft or flexible. In no cyperaceous fruit is the outer tissue flexible at maturity, and in several of his examples the space between the outer wall and the pericarp is filled with parenchymatous tissue, so it is no bladder at all. Thus Koyama (1971: 606) states that in Lagenocarpeae other than *Trilepis*, *Coleochloa*, *Afrotrilepis*, and *Microdracoides*, "the utricles cannot be readily recognizable since the utricles are so completely adnated to the achene pericarp that no superficial distinction can be made between the two organs (Figs. 5 & 8)." There must be some mistake in the figure reference since his Figs. 5 (*Lagenocarpus*) and 8 (*Hypolytrum*, which, by the way, is not a Lagenocarpeae) show sections of fruits in which the outer wall and the pericarp are very distinct. In the 1969 paper they are also distinct for the same two genera in his Figs. 39, 40.

flowers and including the tribes Sclerieae (including Bisboeckelereae), Lagenocarpeae, and Mapanieae.

GROUP VI

The inflorescence is composed of one or more spikelike structures on a culm. Kükenthal (1909) calls each of these a "spicula propria" or simply "spicula." When there is only one, its axis is the tip of the culm itself. In *Schoenoxiphium* and *Kobresia* (Fig. 38A) the spikelike structure is made up of a rachis basally bearing lateral bisexual spikelets ("partial inflorescences") and, apically on the same rachis axis, lateral male flowers. Both the spikelets and male flowers are subtended by glumelike bracts. (The male flowers on the rachis are absent in one species of *Kobresia*.) The spikelike structure, therefore, is technically not a spike although it is often called such, but rather a condensed spikelike panicle. Each lateral bisexual spikelet has a rachilla with a single basal lateral female flower in the axil of a clasping enrolled lamina, generally considered a prophyll, whose lateral margins are fused below, and several apical lateral male flowers in the axils of glumes. The rachilla is a thick, long, visible structure in *Schoenoxiphium*, or a thin, very short, almost invisible structure in *Kobresia*. The male flowers in the spikelets may be reduced to one or be absent; this is rare in *Schoenoxiphium* but common in *Kobresia*. When all the male flowers in a spikelet are absent, the bisexual spikelet becomes female by reduction. Kükenthal calls each of these lateral spikelets which bears a pistil a "spicula partialis" but he also applies the same term to the apical portion of the spikelike structure that bears male flowers directly on its own rachis. This is confusing because these two positions for male flowers are on axes of different branch orders.

In *Uncinia* (Fig. 38B) the spikelike structure is the same, with apical male flowers and basal lateral spikelets. In this genus, however, the lateral spikelets are always purely female, never bearing male flowers. The rachilla extends beyond the orifice of the utricular lamina (perigynium, generally considered a prophyll) and is provided with a hook made by a transformed glume (Snell, 1936; Mora Osejo, 1966), or in one species by the tip of the rachilla itself (Kukkonen, 1967). The hook is used for disseminating the fruit by sticking to the feathers of birds or the fur of mammals.

In *Carex* (Figs. 38C–38H) the spikelike structure has several patterns of flower arrangement. Its axis (rachis) bears lateral male flowers directly and female spikelets laterally, both in the axils of glumelike bracts. The female spikelets may be all grouped together (1) along the basal portion of the spikelike structure (in which case the structure is called "androgynous," or by Kükenthal, "hypogyna"), (2) along the apical portion ("gynaecandrous" or "acrogyna"), (3) in the middle portion with male flowers above and below ("mesogyna"), (4) on both the apical and basal portions with male flowers in the middle ("mesandra"), or (5) the female spikelets may be intermixed singly and alternately along the spikelike structure with male flowers ("alternans"), finally, (6) the male flowers may be on separate spikelike structures from the fertile spikelets ("unisexual," the species usually monoecious, rarely dioecious). The rachilla of the female spikelet bears a single lateral female flower (pistil) in the axil of a utricular

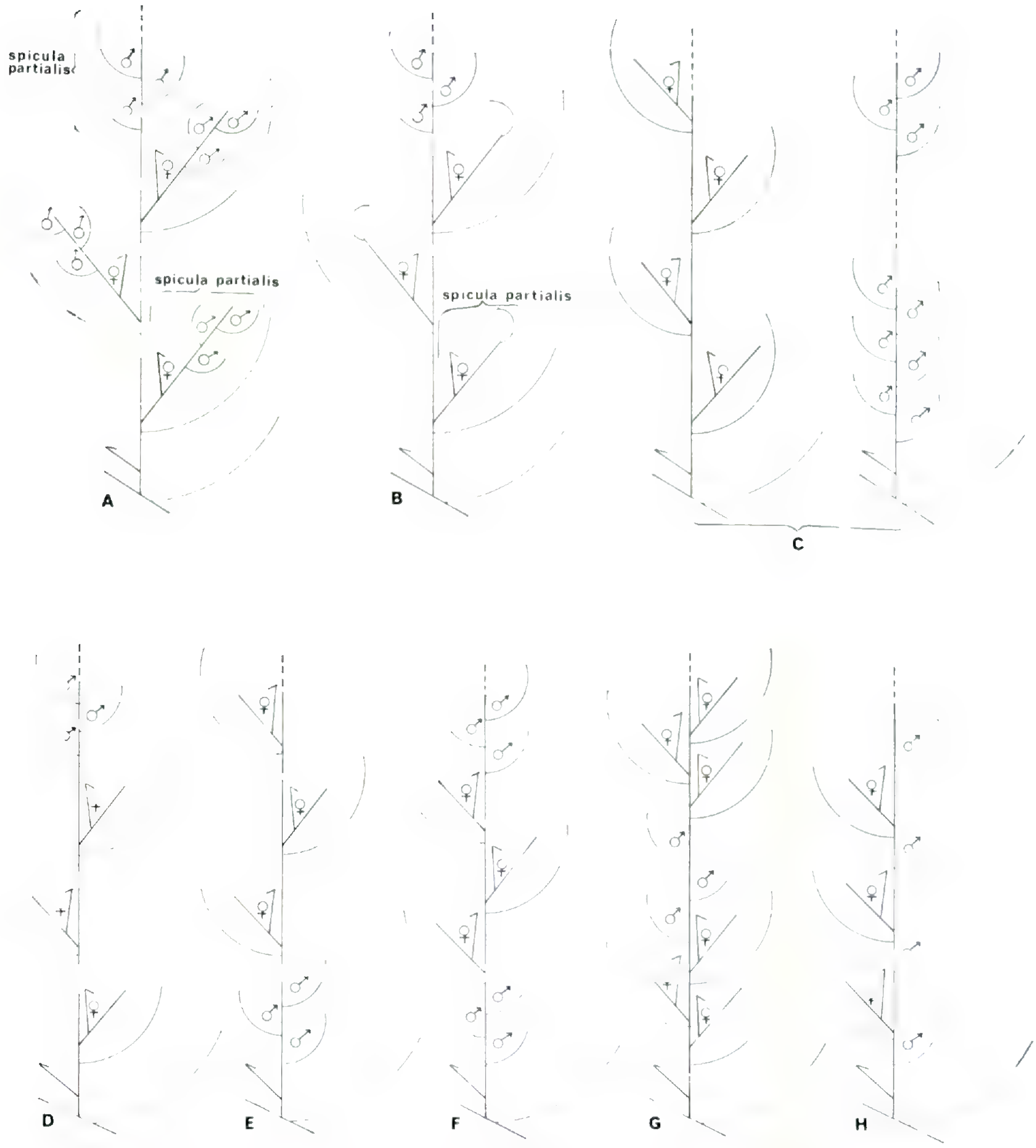

FIGURE 38. Branching patterns of the spikelike structures ("spiculae propriae") in genera of Group VI. The male flowers on the central rachis together form a single "spicula partialis," and each lateral bisexual or female spikelet is also a "spicula partialis" in the terminology of Kükenthal. The number of male flowers and of spikelets on a rachis, as well as the number of male flowers on the rachilla of a bisexual spikelet, varies among different species, individuals and spikelets. A conventional number of these units is shown here.—A. *Schoenoxiphium* and *Kobresia*.—B. *Uncinia*.—C–H. *Carex*.—C. Unisexual.—D. Androgynous or hypogynous.—E. Gynaecandrous or acrogynous.—F. Mesogynous.—G. Mesandrous.—H. Alternate.

lamina (perigynium, generally considered a prophyll). In one species, *C. sitchensis* Prescott ex Bong., as a usual feature (Clarke, 1909; Kükenthal, 1909), and in other species occasionally as teratological events, the rachilla may be prolonged beyond the base of the pistil and bear glumes and a male flower. In a few species the rachilla may be more or less prolonged beyond the base of the pistil although not bearing glumes or male flowers (especially *C. microglochin*

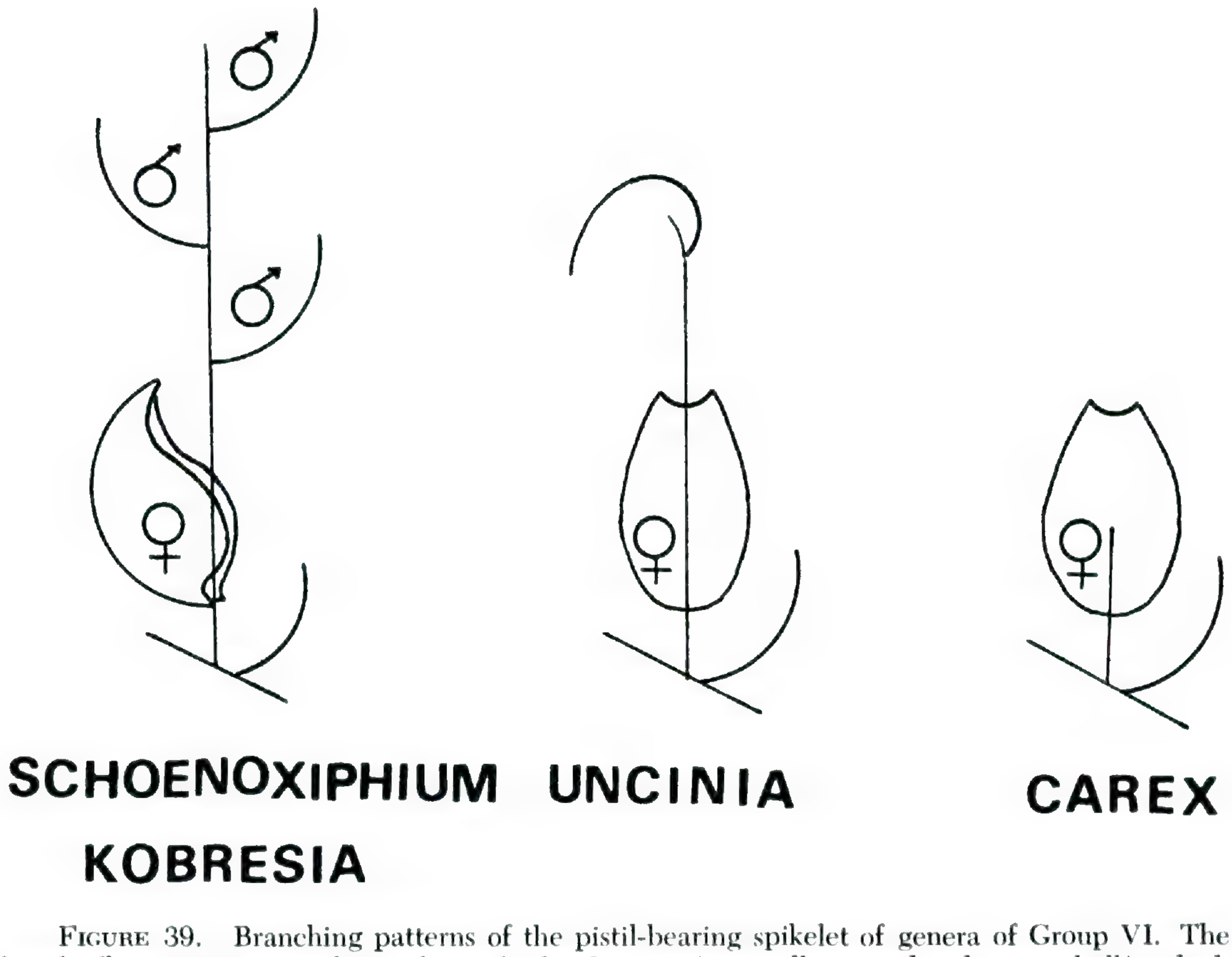

Figure 39. Branching patterns of the pistil-bearing spikelet of genera of Group VI. The female flower is apparently in the axil of a lamina (generally considered a prophyll) which is partially (*Schoenoxiphium* and *Kobresia*) or completely (*Uncinia* and *Carex*) transformed into a utricle.

Wahlenb. where it is exserted from the orifice of the perigynium). In the vast majority of species of *Carex* the rachilla is not prolonged so that the pistil appears to be terminal on it.

Thus, among the four genera, the spikelet containing the pistil forms a somewhat uneven reduction series from *Schoenoxiphium* to *Carex* (Fig. 39).

The assumption that the basal clasping or utricular lamina on the female flower-bearing rachilla is really a prophyll, and that the female flower is really borne in its axil, makes the Cariceae different from all other tribes of the Cyperaceae. For in no other tribe does a prophyll of the rachilla axis, occurring immediately below a true spikelet, bear a flower or indeed any axis at all in its axil. (I consider the two basal, lateral, folded, keeled laminas in the Mapanieae pseudanthium, which in most genera bear male flowers of one stamen in their axils, to be glumes, not prophylls. Paired, opposite, lateral prophylls are typical of the dicots, but do not occur otherwise in the Cyperaceae, and, in fact, are extremely rare in the monocots in general; the only example I know of is in *Dioscorea* (Arber, 1925: 132, fig. civ, 4), where they may more properly be said to be subopposite, and do not bear flowers in their axils.) Therefore, it is necessary to make an exception for the Cariceae and consider the prophyll in this tribe

to be part of the spikelet. So far, neither of the above two assumptions can be excluded, but the subject should be studied further to see if they are indeed true.

Two kinds of ultimate inflorescence unit are defined for Group VI: (1) The female flower-bearing rachilla with its distal male flowers, if any, and with its basal clasping or utricular prophyll, plus the subtending bract of the rachilla. (2) Each single male flower on the rachis of the spike (when this occurs) plus its subtending bract.

Kukkonen (1967) believes that in *Uncinia* the stipe below the pistil bears the pistil terminally and that the continuation of the rachilla is a new branch, that is, the stipe plus the branch that forms the hook is a sympodial axis. Therefore, the perigynium is not the prophyll bearing a lateral pistil in its axil but the subtending bract of the new branch. If this were true for *Uncinia*, it would probably be true for the rest of the Cariceae also. However, the only evidence he gives for this contention is the fact that the central vascular strand (several bundles pressed together) in the stipe below the pistil is thick and goes in a straight line to the pistil, while the two (or in *U. kingii* Boott, one) vascular strands that go to the continuation of the rachilla are thin traces that diverge laterally from the thick central strand. This, however, proves nothing about which of the two branches (that to the continuation of the rachilla and that to the pistil) is the true continuation of the basal part of the thick strand and which is a new branch, since the branching pattern in the two cases is topologically the same. The thickness of a vascular strand is related to the size and rapidity of growth of the organ it supplies, and its orientation (straight or eventually bent) depends on the relative position of the organ it supplies as this is affected by compression or by the necessity of an organ to be in a particular position for functioning, etc. In primitive vascular plants with protosteles and siphonosteles in the stem, a new branch can usually be told from the continuation of the old axis by the pattern of vascularization alone, but this is not always possible in dictyosteles and, by the usual methods of investigation, is impossible to distinguish in the so differently vascularized monocot shoots, particularly in the graminoids, which are highly specialized monocots. It is impossible in the present case to make the distinction in these highly reduced ultimate inflorescence units of graminoids. Proof in this case must be based on prophylls when they exist, or on the branching pattern in lower orders of the inflorescence and the vegetative part of the plant where axes are thicker, internodes are longer, and leaf laminas are larger and more characteristic of what they really are.[5]

[5] Anatomy is no help in this case when the usual methods of investigation are employed. Large monocots have thousands or tens of thousands of vascular bundles at any one level in a stem. Using an elaborate set-up of a specially constructed microtome and movie cameras, Tomlinson (1970) and Zimmermann & Tomlinson (1972, see bibliography for their earlier detailed papers) followed many individual bundles for long distances in the stem and traced their branchings and connections. By this analysis, one can tell a stem branch from a continuation of the old stem axis. However, to be of use in cyperaceous spikelets, a similar investigation would have to be made of the vascular pattern and connections of single bundles in the culms and then in the rachillas to see if the vascular patterns of stems and branches of the large monocots are preserved in these more highly reduced and modified structures. Only if they are could anatomy distinguish a monopodial rachilla from a sympodial pseudorachilla.

Group VI is exemplified by: **Schoenoxiphium*, **Kobresia* (including *Elyna*, *Hemicarex*), *Uncinia*, and *Carex*.

The genera of this group belong to the tribe Cariceae.

CONCLUSIONS

In this paper, entities at three levels have been discussed: (1) the *actual branching patterns* and sex of flowers in sedge inflorescences, of which examples of the last few branch orders are given or referred to; (2) the *definition* of "ultimate inflorescence unit" for the several cases; and (3) the *definition* of "spikelet." An ultimate inflorescence unit may be made up of a single spikelet, or of one or more spikelets plus other axes and laminas, or of a structure not yet considered to be a spikelet (as defined here) because its apparently terminal pistil has not yet been proved to be lateral. For these reasons it has been necessary to distinguish "ultimate inflorescence unit" from "spikelet" and to erect classes of the former as an aid in making subdivisions of the family.

The inflorescence patterns, along with other characteristics, allow grouping of the genera into tribes. The family may be divided into tribes directly or, if there seems to be a natural grouping of tribes, into subfamilies first. I believe subfamilies are possible and offer the following scheme with included tribes (plus *Dulichium* and *Scleria* whose tribal position is still uncertain).

1. Cyperoideae (= Rhynchosporoideae)

True bisexual flowers arranged in true, racemosely-branched spikelets. In the Rhynchosporeae as a regular feature and sometimes in the other tribes, one or more flowers in a spikelet are male. Tribes Scirpeae, Cypereae, Rhynchosporeae, and *Dulichium*.

2. Caricoideae

True, always unisexual flowers in true, racemosely-branched spikelets. Tribes Lagenocarpeae, Bisboeckelereae, Cariceae, and *Scleria*.

3. Mapanioideae

Flowers always unisexual, male flowers always with only 1 stamen; female flowers each joined with 2 or more male flowers to form a pseudanthium; rarely (*Syntrinema*) the female flower of a pseudanthium may be absent. Inflorescence on a culm rarely of only 1 terminal pseudanthium (*Chrysithrix*); usually inflorescence of 1 or more pseudospikelets each made up of (1–)2– many pseudanthia racemosely arranged on a rachis. Tribes Mapanieae, Syntrinemeae, Micropapyreae.

After this study of branching patterns of the ultimate units of the inflorescence, I find that there are still three problems to be resolved in the Cyperaceae as a whole.

1. Are the structures which appear to be simple bisexual flowers really true flowers or are they pseudanthia (synanthia)?

2. Are the apparently terminal female flowers really terminal or are they lateral (pseudoterminal)?

3. Are the apparent rachillas (lacking recognizable prophylls along their length) monopodial (true rachillas) or sympodial (pseudorachillas)?

Literature Cited

Arber, A. 1925. Monocotyledons, a Morphological Study. University Press, Cambridge. [Reprint, 1961, Stechert, New York.]

Barros, E. 1947. Cyperaceae. *In* H. R. Descole, Genera et Species Plantarum Argentinarum. Vol. 4 (2 parts). Institutionis Michaelis Lillo, Buenos Aires.

Bentham, G. 1883. Cyperaceae. *In* G. Bentham & J. D. Hooker, Genera Plantarum. Vol. 3: 1037–1073. L. Reeve & Co., London.

Celakovsky, L. 1887. Ueber die ährchenartigen Partialinflorescenzen der Rhynchosporeen. Ber. Deutsch. Bot. Ges. 5: 148–152.

Clarke, C. B. 1909. Illustrations of Cyperaceae. Williams & Norgate, London.

Eiten, L. T. 1976. The morphology of some critical Brazilian species of Cyperaceae. Ann. Missouri Bot. Gard. 63: 113–199.

Goebel, K. von. 1888. Über den Bau der Ährchen und Blüter einiger javanischer Cyperaceen. Ann. Jard. Bot. Buitenzorg 7: 120–140.

Holttum, R. E. 1948. The spikelet in Cyperaceae. Bot. Rev. (Lancaster) 14: 525–541.

Kern, J. H. 1961. Cyperaceae of Thailand (excl. *Carex*). Reinwardtia 6: 25–83.

Koyama, T. 1961. Classification of the family Cyperaceae (1). J. Fac. Sci. Univ. Tokyo., Sect. 3, Bot. 8: 37–148.

———. 1967. Cyperaceae-Mapanioideae. Mem. New York Bot. Gard. 17: 23–79.

———. 1969. Delimitation and classification of the Cyperaceae-Mapanioideae. Pp. 201–228, *in* J. E. Gunckel (editor), Current Topics in Plant Science. Academic Press, New York.

———. 1971. Systematic interrelationships among Sclerieae, Lagenocarpeae and Mapanieae (Cyperaceae). Mitt. Bot. Staatssamml. München 10: 604–617.

——— & B. Maguire. 1965. Cyperaceae tribe Lagenocarpeae. Mem. New York Bot. Gard. 12: 8–53.

Kükenthal, G. 1909. Cyperaceae-Caricoideae-Cariceae. *In* A. Engler (editor), Das Pflanzenreich. IV. 20 (Heft 38): 1–824.

———. 1935–1936. Cyperaceae-Scirpoideae-Cypereae. *In* A. Engler (editor), Das Pflanzenreich. IV. 20 (Heft 101): 1–671.

Kukkonen, I. 1967. Spikelet morphology and anatomy of *Uncinia* Pers. (Cyperaceae). Kew Bull. 21: 93–97, *pl. 6.*

Mora, L. E. 1960. Beiträge zur Entwicklungsgeschichte und vergleichenden Morphologie der Cyperaceen. Beitr. Biol. Pflanzen 35: 253–341.

Mora Osejo, L. E. 1966. Inflorescencias parciales de *Uncinia* y agrupación de las Caricoideae. Caldasia 9: 277–293.

Nees von Esenbeck, C. G. 1842. Cyperaceae. *In* C. F. P. von Martius (editor), Flora Brasiliensis 2(1–3): 1–357. Leipzig.

Palla, E. 1905. Über den morphologischen Wert der Blüte der Gattungen *Lipocarpha* und *Platylepis*. Ber. Deutsch. Bot. Ges. 23: 316–323.

Pax, F. 1886. Beiträge zur Morphologie und Systematik der Cyperaceen. Bot. Jahrb. Syst. 7: 287–318, *Taf. II.*

———. 1887. Cyperaceae. *In* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien 2 (2): 98–126.

Raymond, M. 1966. Studies in the flora of Thailand. Cyperaceae. Dansk Bot. Ark. 23: 311–374.

Robinson, E. A. 1966. A provisional account of the genus *Scleria* Berg. (Cyperaceae) in the Flora Zambesica area. Kew Bull. 18: 487–551.

Schultze-Motel, W. 1959. Entwicklungsgeschichtliche und vergleichend-morphologische Untersuchungen im Blütenbereich der Cyperaceae. Bot. Jahrb. Syst. 78: 129–170, *Taf. 4–5.*

———. 1964. Reihe Cyperales. *In* H. Melchior (editor), A. Engler's Syllabus der Pflanzenfamilien. Ed. 12. Vol. 2: 602–607.

Schulz, A. 1887. Zur Morphologie der Cariceae. Ber. Deutsch. Bot. Ges. 5: 27–43.

Snell, R. S. 1936. Anatomy of the spikelets and flowers of *Carex*, *Kobresia* and *Uncinia*. Bull. Torrey Bot. Club 63: 277–295.

TOMLINSON, P. B. 1970. Monocotyledons—Towards an understanding of their morphology and anatomy. *In* R. D. Preston (editor), Advances in Botanical Research. Vol. 3. Academic Press, New York.

TROLL, W. 1964. Die Infloreszenzen: Typologie und Stellung im Aufbau des Vegetationskörpers. Band I. Gustav Fischer Verlag, Stuttgart.

ZIMMERMANN, M. H. & P. B. TOMLINSON. 1972. The vascular system of monocotyledonous stems. Bot. Gaz. (Crawfordsville) 133: 141–155.

THE MORPHOLOGY OF SOME CRITICAL BRAZILIAN SPECIES OF CYPERACEAE[1]

Liene Teixeira Eiten[2]

Abstract

Eight taxa comprising six Brazilian species of Cyperaceae originally described in six different genera are redescribed in detail from the type collections and amply illustrated. Incorrect data and interpretations by the original authors are corrected.

Syntrinema brasiliense Radlk. & Pfeiffer is accepted as an independent genus and species. The original description of the inflorescence units was based on material which is not of this genus. The genus has pseudanthia, but these are of a type not found in the Mapanieae (the only tribe of Cyperaceae up to now known to have undoubted pseudanthia). The genus is placed in the newly described tribe, Syntrinemeae. Besides bisexual pseudanthia, the pseudospikelets also contain male pseudanthia lacking pistils and possibly neutral ones also. Instead of laminar glumellas as in the Mapanieae, the glumellas are bristles.

Chamaegyne pygmaea Süss. is shown to be a new species of *Eleocharis* series *Tenuissimae*, *E. chamaegyne* L. T. Eiten. The basal laminas that form the tiny tufts are not vegetative leaves but glumes and associated scales of the basal spikelets.

Helonema estrellense Süss. is shown to be an aquatic phase of *Eleocharis minima* Kunth. Topotype material collected and cultivated submersed in an aquarium retained the flaccid, filamentous *Helonema* vegetative form and remained sterile. When cultivated in moist soil and allowed to grow in the air, ramets of the same topotype clone formed small tufts of typical *Eleocharis minima* with abundant ripe achenes.

Bisboeckelera paporiensis Süss. is shown to be *Diplacrum longifolium* because the glume-like scales which enclose the pistils are free as in *Diplacrum*; the pistil is not enclosed in a utricle as in *Bisboeckelera*.

Micropapyrus viviparoides Süss. is accepted as an independent genus and species, and is put into the newly described tribe, Micropapyreae, because its pseudanthia are different from both the Mapanieae and from *Syntrinema*. Its glumellas are bristles.

The New World *Websteria submersa* (C. Wright) Britton is considered to be conspecific with the Old World *Scirpus confervoides* Poiret under the combination *Websteria confervoides* (Poiret) Hooper, and the varieties *W. submersa* var. *negrensis* Süss. and *W. submersa* var. *luetzelburgii* Süss. are not recognized.

Among the many existing problems in the family Cyperaceae, that of the branching patterns of the ultimate units of the inflorescence are particularly important since the correct subdivision of the family must be largely based on this character. Of the six species chosen for exposition in this article, three are known only from the type collection in one herbarium. Another species, although widespread and common in its terrestrial form, also occurs as a very different looking aquatic form which has been rarely collected and has been described as a new genus. The only descriptions of these four taxa are the original ones, which are confused and full of errors, making it impossible to recognize the true structure of the inflorescence. The fifth species is rare in herbaria; the sixth is

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[1] I wish to thank Dr. George Eiten for translating this paper to English and for providing the Latin descriptions; Dr. J. Murça Pires for the loan of Cyperaceae from the Instituto Agronômico do Norte, Belém, Pará; and the director of the Staatsherbarium München for the loan of types. Dra. Rosa Vilani Drummond kindly cared for the clones of the topotypes of *Helonema* which were planted at the agricultural station at Km 47, Rio de Janeiro State. During 1974, this work was supported by a grant from the Conselho Nacional de Pesquisas.

[2] Universidade de Brasília, Brasília, DF, Brasil.

Ann. Missouri Bot. Gard. 63: 113–199. 1976.

FIGURE 1. Lectotype of *Syntrinema brasiliense* Radlk. & Pfeiffer, *Luetzelburg 15484*; × 0.4. (For "Holotypus" on annotation label, read "Lectotypus.") The following drawings of this species, Figs. 4–20, were made from plants of this sheet.

2 3

FIGURES 2–3. Syntypes of *Syntrinema brasiliense* Radlk. & Pfeiffer; × 0.2—2. *Luetzelburg 1223.*—3. *Luetzelburg 15843.*

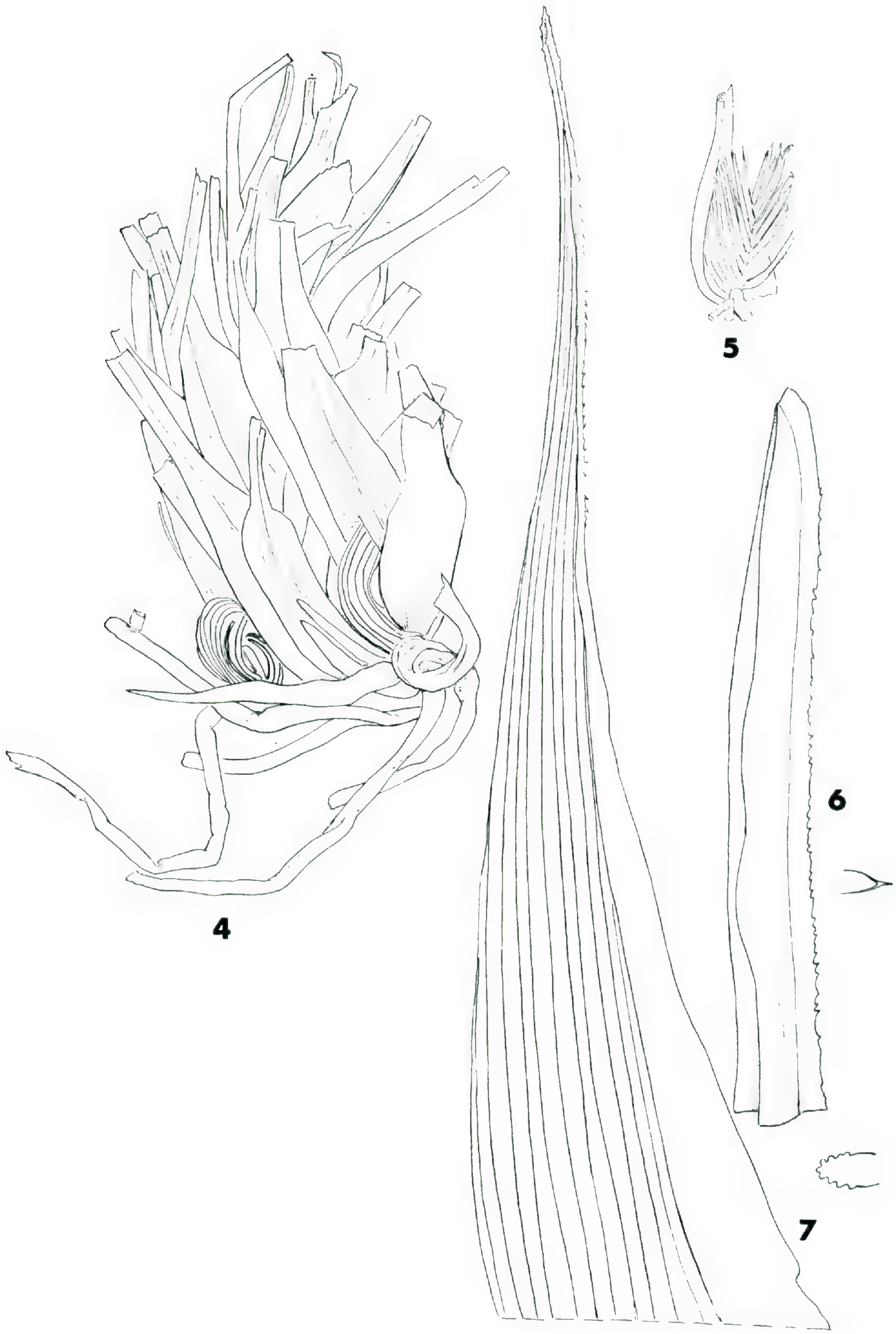
a common species but the variety of branching patterns in its inflorescence has never been described before.

The selected taxa illustrate the range of problems which a cyperologist may encounter in his study of the morphology of the family. An extreme ecological situation may radically change the habit of the plant, the number of glumes and flowers in the spikelet, and affect the sex of the flowers (*Helonema estrellense* Süss.). Plants which have suffered these modifications cannot be correctly identified based only on herbarium material; it is necessary to cultivate the plant in different conditions to produce structures which are more typical of the species.

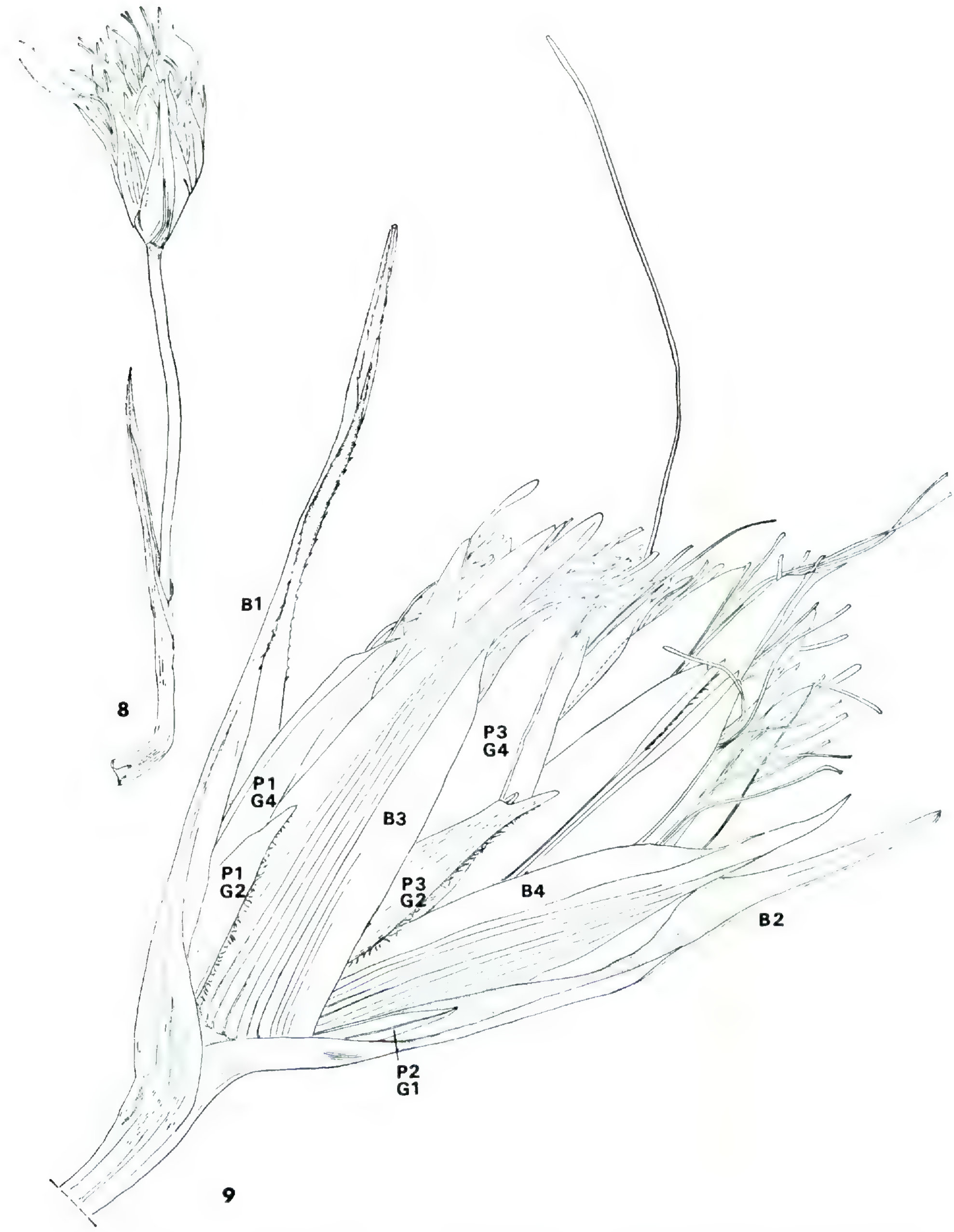
Variability in the composition of the spikelet in the same individual (*Helonema estrellense*) or in the branching pattern of the ultimate inflorescence units (*Bisboeckelera paporiensis* Süss.) requires that many parts of an inflorescence be analyzed.

Types of inflorescence branching patterns which are new for the family may be found (*Syntrinema brasiliense* Radlk. & Pfeiffer, *Micropapyrus viviparoides* Süss.), a possibility still open for material from little collected regions. Discoveries of this type may necessitate changes or additions in the higher units of subdivision of the family.

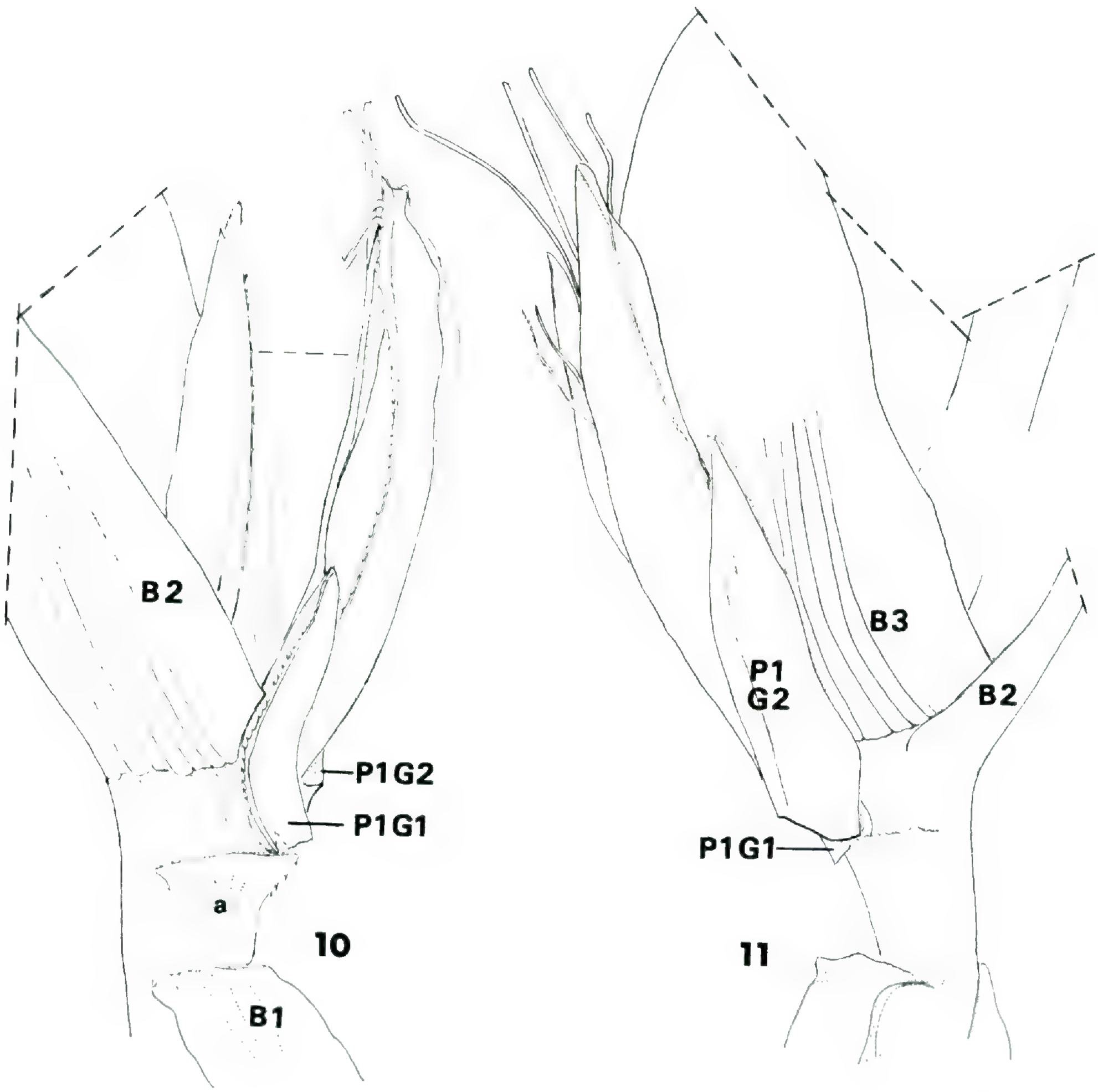
The validity of infraspecific taxa, such as varieties of *Websteria confervoides*



Figures 4–7.—4. Base of clump showing thick roots, two small shoots, and leaf bases; × 1.1.—5. Adaxial view of a small shoot and the base of its subtending leaf; × 1.1.—6. Upper part of a basal leaf of a small shoot showing naviculate form (open to left), with rounded apex and winged, denticulate keel at right; × 16. To the right is a cross section.—7. Upper part of an apical leaf of a small shoot showing canaliculate dorsal surface, membranous margin, and acuminate apex; × 16. To the right is a cross section.



FIGURES 8–9.—8. Peduncle (culm) with tubular prophyll and capitate inflorescence; × 1.4.—9. Capitulum; × 10.4. B1 = bract subtending first (lowest) pseudospikelet. B2–B4 = bracts subtending the second, third and fourth pseudospikelets, respectively. P1G2 = second glumiform bract of the first pseudospikelet; P1G4 = fourth glumiform bract of the first pseudospikelet; P2G1 = first glumiform bract (prophyll) of second pseudospikelet; P3G2 and P3G4 = second and fourth glumiform bracts of the third pseudospikelet. Note elongated filaments (from which the anthers have fallen) exerted from the tips of the pseudospikelets.

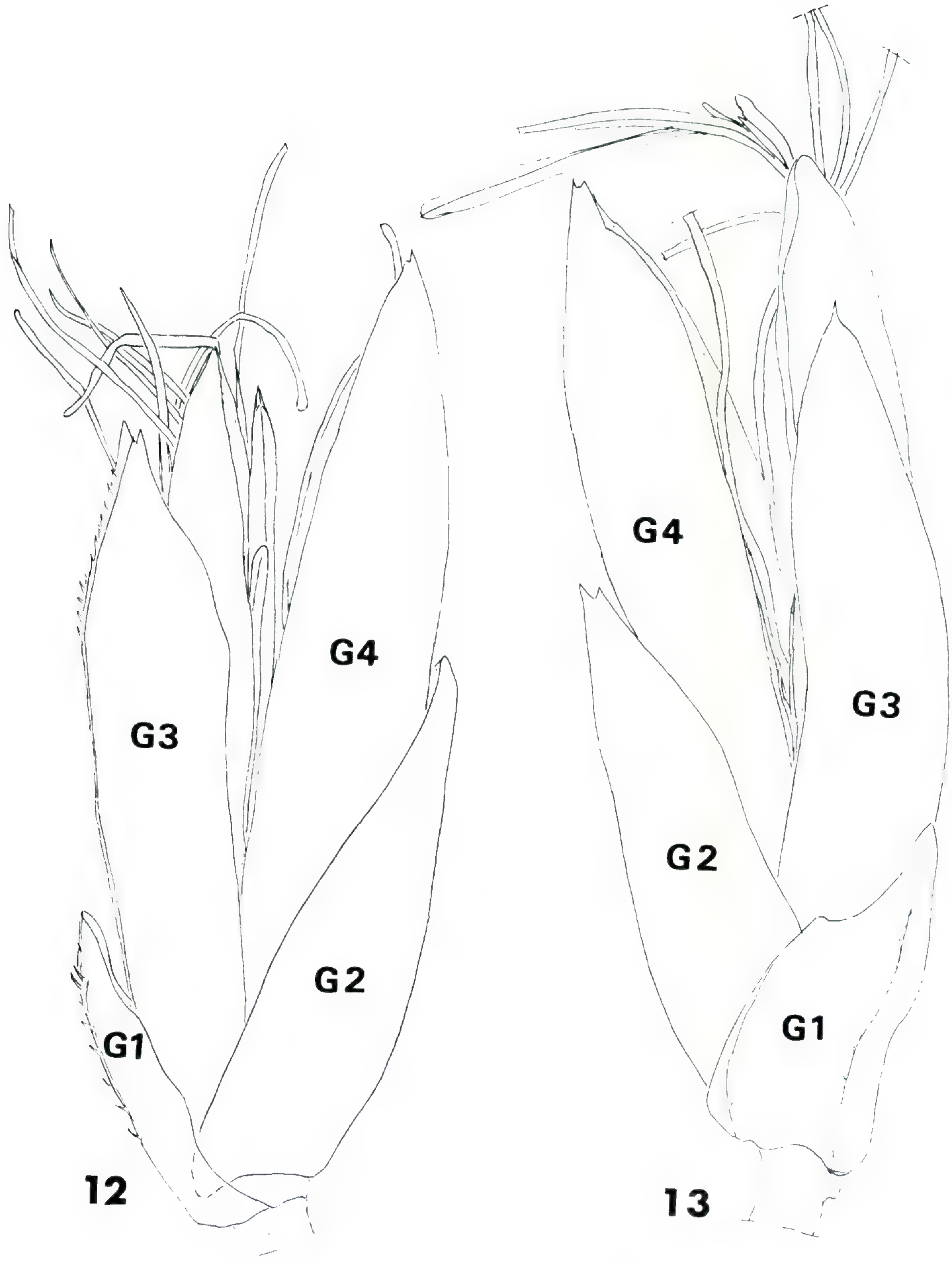


Figures 10–11. Base of capitulum shown in Fig. 9; × 15.—10. Bract B1 has been lowered and partially torn from its axis, leaving the scar, a. This bract subtends the lowest pseudospikelet in the head, shown on the right side. The level of emergence of bract B2 is further up the axis of the capitulum than that of B1.—11. Other side of the same capitulum, showing the level of emergence of bract B2 above that of B1.

(Poiret) Hooper (including *W. submersa* (C. Wright) Britton), can only be resolved by studying a sufficient number of collections from over the range of the species to see whether gaps in the variation pattern are sufficiently great.

There are cases where a collection represents a distinct species which shows a certain relationship to a known genus without falling into it perfectly. It then becomes necessary to decide whether to widen the morphological limits of the genus to include this species or to establish a new genus for it (*Chamaegyne pygmaea* Süss.).

As a result of this morphological study, I present new descriptions of type collections in which structures have been badly described in the original publica-



FIGURES 12–13. Abaxial and adaxial views of pseudospikelet P1 showing gluniform bracts G1 (prophyll), G2, G3, and G4; × 20. The prophyll and G2 are empty. Note prophyll G1 with its two characteristic veins and retuse apex.

tions. When it has been necessary to correct the identification of the material examined, the correct name of the species is given in parentheses below the name of the type, at the beginning of each description.

The *Chamaegyne*, *Helonema*, *Bisboeckelera* and *Websteria* collections were

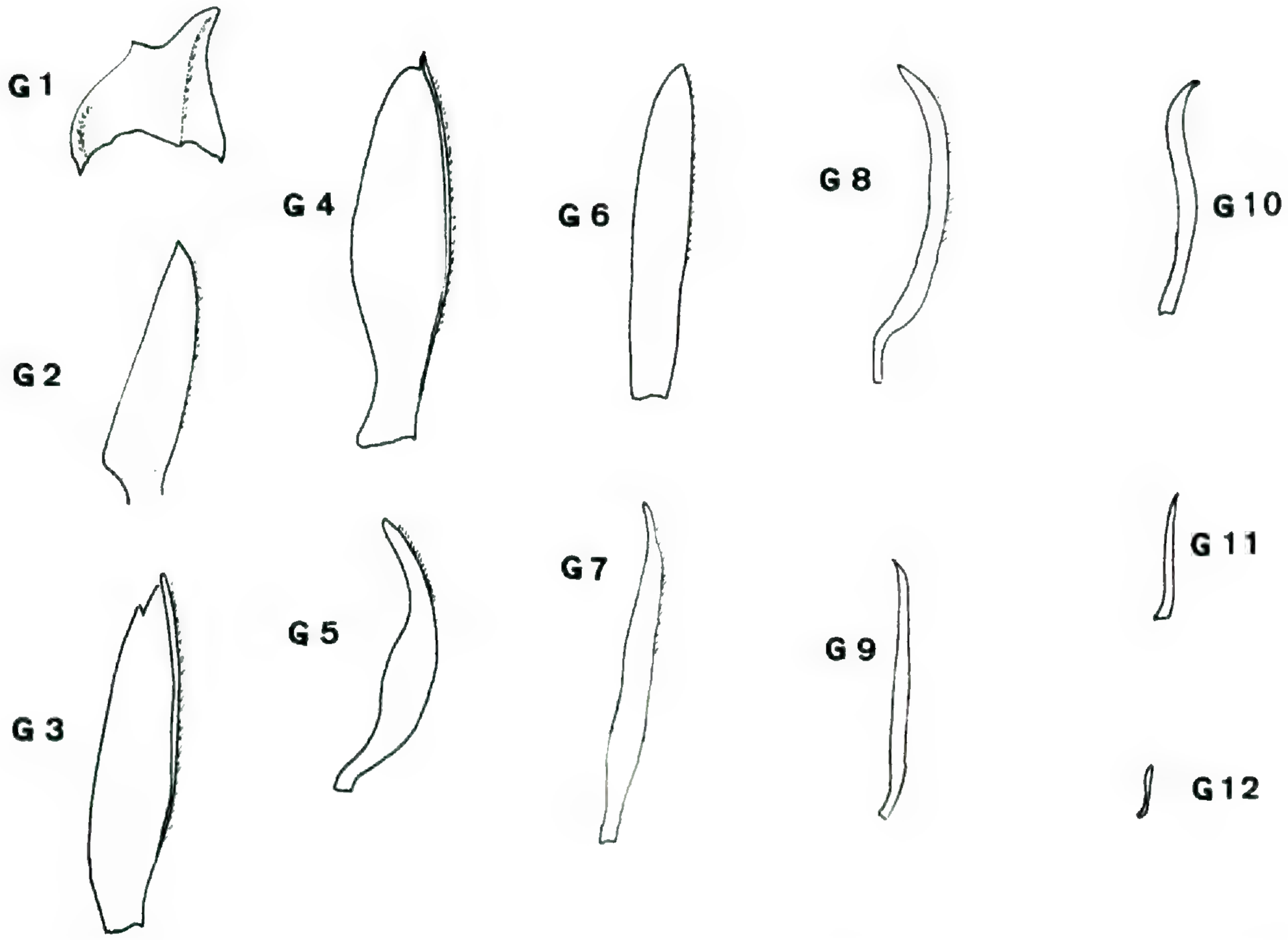


FIGURE 14. Glumiform bracts of pseudospikelet P1 arranged in order from base to apex; × 4.4. G1 is the prophyll, shown in abaxial view. G2 to G12 are in lateral view, opening to the left and with the midvein to the right.

treated in a brief preliminary fashion without illustration in Eiten (1970, 1972). Along with *Syntrinema* and *Micropapyrus* they are here treated much more fully.

In the descriptions and discussions which follow, a basic distinction is made between "terminal" and "lateral" flowers. Clearly, every flower is terminal in relation to the stem whose tip is its floral axis. Therefore, a lateral flower is lateral in relation to another stem from which the floral axis stem arises, which in the case of true spikelets is the rachilla. In the one-flowered spikelets of certain species of *Cyperus* (sensu lato), *Eleocharis*, and other genera, most of whose species have many-flowered spikelets, the flower seems terminal on the rachilla although, by comparison with related species, it is obviously really lateral, that is, pseudoterminal. The case is not so clear in the Mapanieae and the Bisboeckelereae, for in these tribes there is an apparently terminal pistil (female flower) on an axis, while lower down on the same axis laterally arise single stamens (male flowers) in the Mapanieae or spikelets of male flowers in the Bisboeckelereae. The Lagenocarpeae are claimed to have a spikeletlike structure with a terminal female flower also; however, evidence has been given in the previous article (Eiten, 1976) indicating that the apparently terminal pistil is actually lateral. I believe that all flowers in the Cyperaceae are basically lateral but this will have to be proved individually for each genus or group of related genera either by direct evidence or by a convincing analogy.

Syntrinema brasiliense Radlk. & Pfeiffer

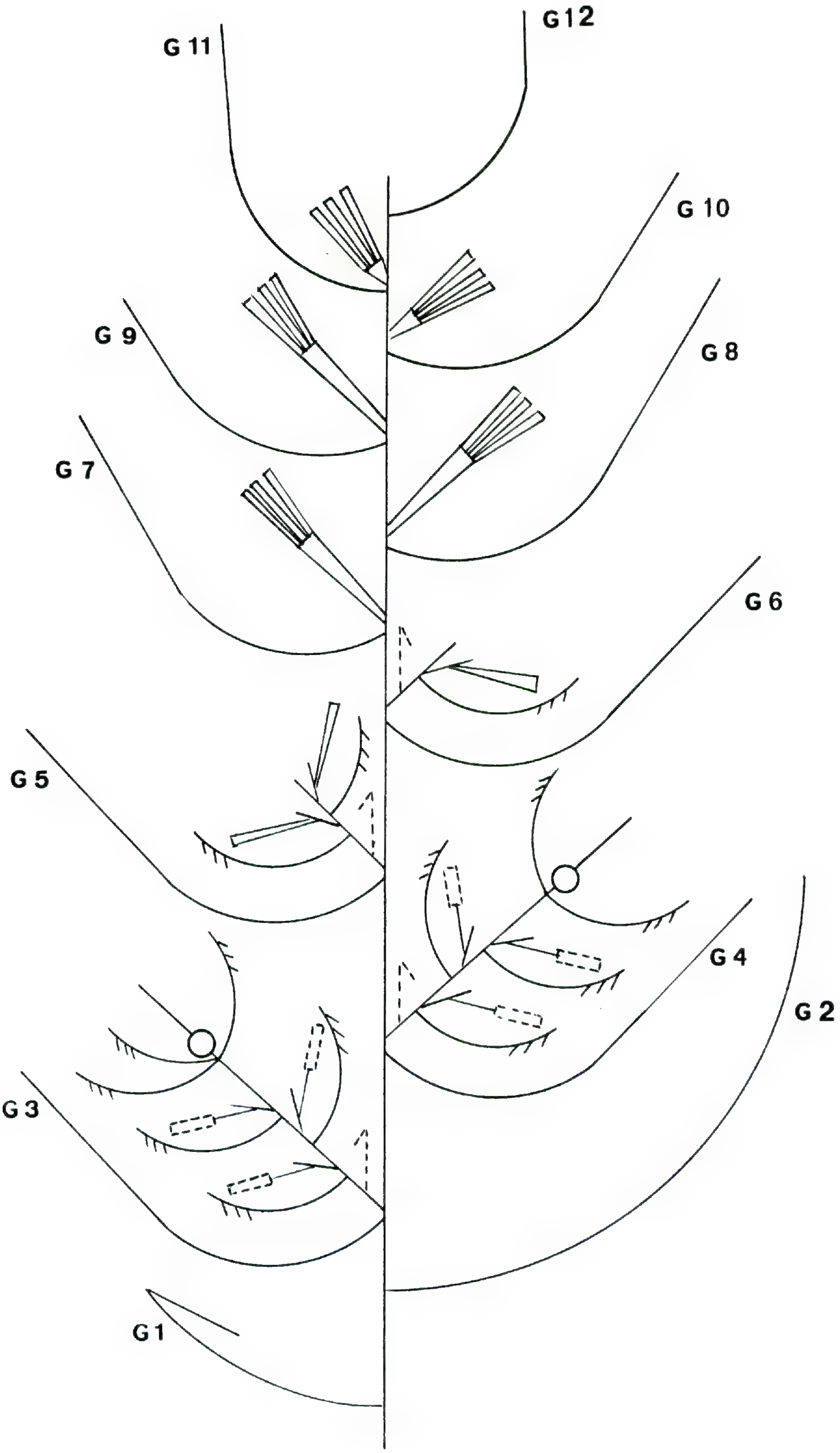
Description of the lectotype of *Syntrinema brasiliense* Radlk. & Pfeiffer, Repert. Spec. Nov. Regni Veg. 21: 238–239. 1925: Brasilia, West Bahia, Campinas Boa Esperança, 1912, *Luetzelburg 15484* (M). Photographs of the other syntypes seen: Brasilia, Goyas, Aug. 1912 *Luetzelburg 15843, 1223* (both M).

The plant forms clumps 10–20 cm tall. The leaves are imbricate and widened at the base. In the collection examined, the apices of the leaves had been destroyed by fire (Figs. 1–4). Straight or curved, small vegetative shoots occur in some leaf axils (Fig. 5); these shoots have two types of leaves, both longitudinally folded and distichously arranged (Figs. 6–7). Each culm bears a tubular prophyll at its base and a capitulum at its apex (Fig. 8). The capitulum is composed of approximately 9 or 10 pseudospikelets arranged spirally on an axis which is the continuation of the culm (Figs. 9–11). A bract subtends each pseudospikelet; the two basal bracts are longer, equalling or exceeding the capitulum (Fig. 9, B1–B2). On the axis of the pseudospikelet there are 11–12 glumiform bracts distichously arranged (Figs. 12–13, G1–G4; 14–15). The two basal bracts and the most distal bract are empty; the others subtend pseudanthia, i.e., very reduced ultimate inflorescence units which look like flowers (Fig. 15). The two lower pseudanthia are bisexual (Figs. 15–16, 21); an apparently terminal pistil is surrounded by 2–3 hypogynous bristles which appear to arise at the same level (Figs. 17–19). Below these bristles there are three more bristles arising at different levels on the rachilla, each subtending a male flower of a single stamen (Fig. 17). A gynophore can be made out attached to the young pistils (Fig. 18) but it is not so visible in the more developed pistils. The style is long and undivided.

The upper pseudanthia lack pistils. The lower two of these have bristles subtending what appear to be the filaments of male monandric flowers (Fig. 15, in the axils of glumiform bracts G5 and G6). In the lower of these two pseudanthia there are two bristles which appear to arise at the same level; in the upper of the two there is only one bristle or none. These bristles are more delicate than those in the bisexual pseudanthia. More material in other stages of flower growth would have to be examined to see if the filaments in these two pseudanthia really bear anthers (which therefore had fallen off in the material seen) and in which case the pseudanthia are male, or whether they are only staminodes in which case the pseudanthia are neutral.

In the more distal pseudanthia there are what appear to be functional male flowers. The pseudanthium consists of a column which is 3-lobed in cross section and which is shorter in the more distal pseudanthia. The column bears three large anthers at its apex (Fig. 20). The column consists of the three filaments fused together; the rachilla and bristles are perhaps also fused with them. Since the stamens in the lower bisexual pseudanthia are clearly each separate flowers, it is highly probable that the three stamens in the upper male pseudanthia are also each a separate male flower although they are fused together by their filaments. A unisexual pseudanthium has not been reported before in the angiosperms so far as I know.

Further details are given in the legends to the figures.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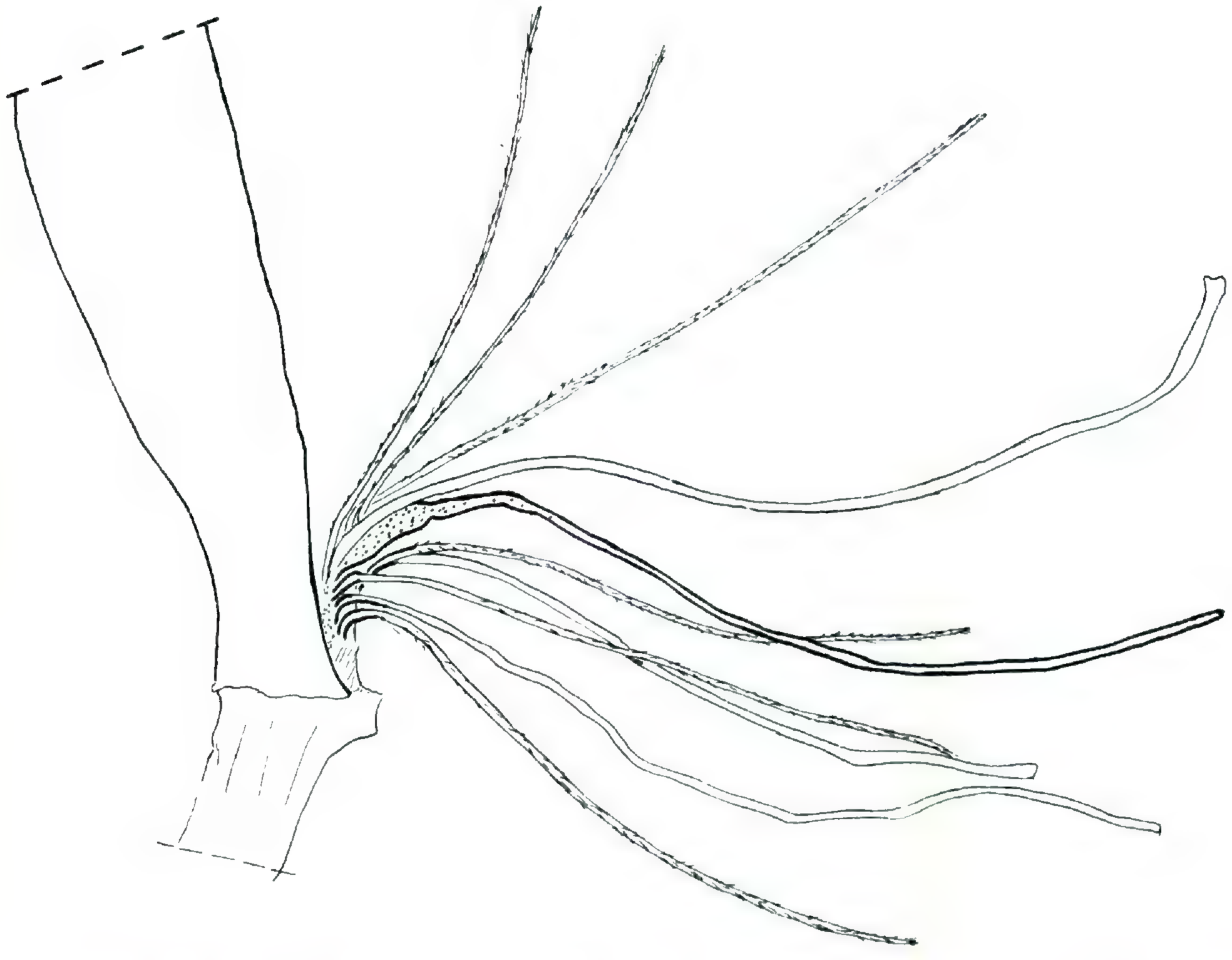

FIGURE 16. Base of pseudospikelet P1; × 25. The basal glumiform bracts, G1, G2 and G3, have been removed showing the lowest pseudanthium, PA1, appearing like a flower. Note 6 pilose bristles, 3 glabrous filaments from which the anthers have fallen, and a young pistil with a narrow ovary and long undivided style.

The genus *Syntrinema* has only one species, S. *brasiliense*, known only from its three syntype collections. The original description of the genus and species contains several errors. After having studied the syntype material, I found that the original description was based on a mixture of plants of different genera. The illus-

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FIGURE 15. Branching pattern of basal pseudospikelet P1. The glumiform bracts, G1 (prophyll) and G2 are empty. Bract G3 subtends the pseudanthium PA1 (illustrated in Figs. 16–19), which has three basal bristles arising at different levels, each subtending a male flower of one stamen from which the anthers had supposedly fallen when the plant was examined, and three bristles at the base of the pistil. The bract G4 subtends the pseudanthium PA2, similar to PA1 but with two hypogynous bristles. Bract G5 subtends an apparently male pseudanthium PA3, which has two bristles and two structures which appear to be thick filaments or fused filaments. Whether these had anthers which fell off or whether anthers never developed is not known for certain. Bract G6 subtends a similar, apparently male pseudanthium PA4, which consists of one bristle and one filament structure similar to that in PA3. Bracts G7, G8, G9 and G10 subtend male pseudanthia, each consisting of a column (3-lobed in cross section) formed by the fusion of three filaments with the rachilla; there may be bristles fused here also. Three free anthers occur at the apex of the column. Bract G11 subtends a similar male pseudanthium but much less developed, with three anthers difficult to distinguish. Bract G12 is reduced and empty and covers over the tip of the pseudospikelet rachis. The pseudospikelet is essentially distichous but sometimes it is difficult to trace the two files of glumiform bracts. The hooked broken lines indicate the position that the prophylls of the pseudanthia would have if they existed.

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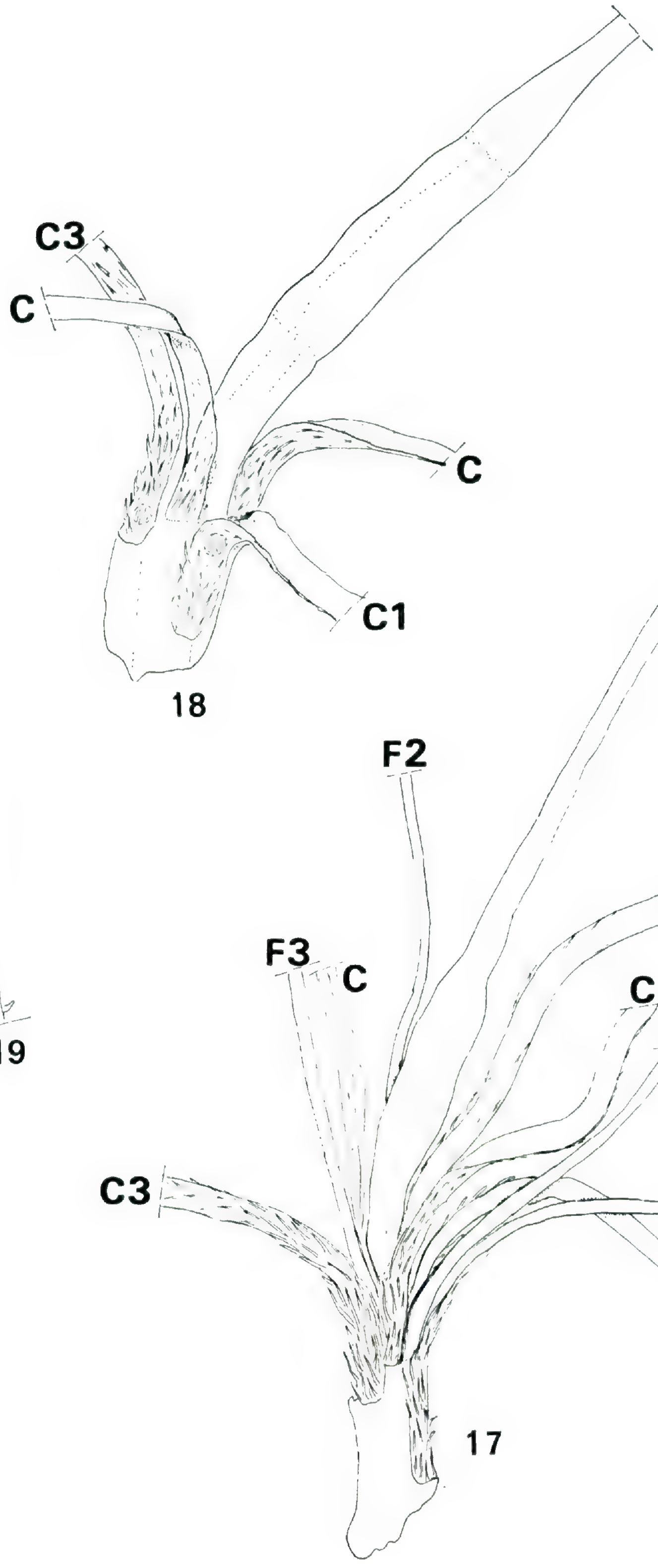
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tration of the habit given in the original publication corresponds to the species treated here. But the description and illustrations of the inflorescence unit are not that of *Syntrinema*. Pfeiffer (1925) gave a floral diagram of a pseudanthium with a terminal pistil surrounded by four empty glumellas and then by eight stamens, each in the axil of a glumella. The arrangement of stamens and glumellas is in a spiral except for the two outermost glumellas which are lateral. The glumellas are illustrated in other drawings in lateral and dorsal views. No bristles are shown. When Pfeiffer described the genus, he clearly stated that *Syntrinema* does not possess bristles ("Setae squamulaeque nullae"). The pistil seen by Pfeiffer has "Ovarium 2-loculare (an semper?)" and the style is distinctly bifid. An ovary with two locules never occurs in Cyperaceae. I suppose that there was a lapse or an error of observation here or the author examined material of another family for this character.

The difference between the characters described by Pfeiffer and those which I found in the type are considerable. The reason for the divergence is that Pfeiffer used material of another genus when he described the inflorescence unit of *Syntrinema*. I found in an envelope glued to the lower left corner of the herbarium sheet of *Luetzelburg 15484* (see Fig. 1) fragments of inflorescence units that were not of *Syntrinema* but which correspond to the drawings and description of the units given by Pfeiffer. The illustrations are of the unit of *Chorizandra*, a genus which does not occur in Brazil. This can be seen by comparing the Pfeiffer drawings with the figures of Tab. CXIX of Clarke (1909). Pfeiffer's Figs. c, d, e and g are respectively equal to Clarke's Figs. 4, 5, 3 (*Chorizandra sphaerocephala* R. Br.) and 11 (*C. enodis* Nees). Pfeiffer's floral diagram (his Fig. b) for S. *brasiliense* corresponds to the floral diagram of *C. sphaerocephala* (Fig. 7 of Clarke) in number and arrangement of parts except for one more stamen in the *Syntrinema* diagram.

In the same article in which Pfeiffer describes *Syntrinema brasiliense*, he included a key to genera of the Mapanieae, to which *Chorizandra* belongs. It is possible that in preparing this key he studied specimens of *Chorizandra* and by mistake returned the examined fragments to the envelope of *Syntrinema*. That his drawings are so similar to those of Clarke that they seem like tracings is even more peculiar.

Syntrinema has been placed under *Rhynchospora*. Ballard (1934) thought that the three syntypes of S. *brasiliense* were a new species of *Rhynchospora*; in

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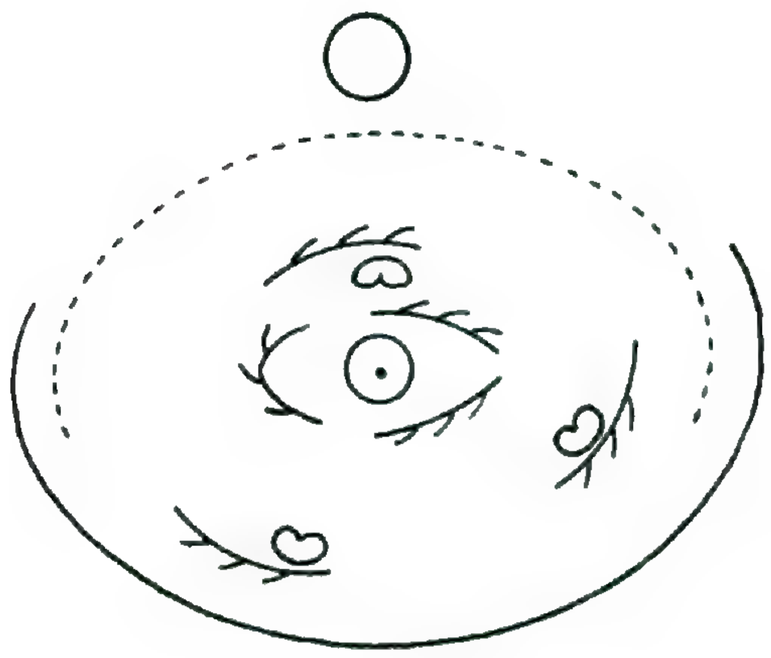
FIGURES 17–19. Details of pseudanthium PA1, showing insertion of bristles and filaments; × 56.—17. Bristles C1, C2, and C3 arise at different levels and subtend filaments F1, F2, and F3. The three upper bristles, C, apparently arise at the same level around the base of the pistil. The filaments are glabrous; the bases of the bristles are pilose on the abaxial side.—18. The two small shaded circles at the base of bristles C3 and C1 indicate the scars left when filaments F3 and F1 were pulled off. The scars are on the axis and in the drawing are seen through the bristle bases. The insertion at the base of the ovary of the bristle C whose base is visible is above that of the insertion of filament F3 which is not shown in this drawing. The base of all the bristles is laminar but the upper part, shown in Fig. 19, is terete. In the pistil in Fig. 18, two transverse lines delimit the young ovary; the axis below the lower line, which supports the ovary, is a gynophore.



Figures 20–21.—20. Three stamens with filaments united into a column; × 25. This constitutes the male pseudanthium PA5.—21. Floral diagram of pseudanthium PA1. Compare with branching pattern in Fig. 15. The upper circle represents the axis of the pseudospikelet; the solid curve is the glumiform bract which subtends the pseudanthium; the broken-line curve represents the position the prophyll would have if it existed. The six hachured lines are bristles, three subtending the male flowers of one stamen and three around the pistil.

1934 he annotated the sheets "*R. confusa* F. Ballard" and published the name. Hutchinson (1959) included *Syntrinema* in the synonymy of *Rhynchospora*. Koyama (1967) recognized *Syntrinema* as a separate genus and placed it in his subtribe Mapaniinae of the tribe Mapanieae. Because of the floral diagram given by Pfeiffer (but which really is of *Chorizandra*) Koyama thought that *Syntrinema* was similar to the genera of the subtribe Chrysitrichinae. Apparently, Koyama's decision was based only on the original description and not examination of the plant because in his article he described the spikelet as given by Pfeiffer.

Syntrinema and *Rhynchospora* are not remotely related. The inflorescence of *Rhynchospora* is composed of true flowers in true spikelets while that of *Syntrinema* is composed of pseudanthia in pseudospikelets. *Syntrinema* is an autono-

mous and distinctive genus. Although it has pseudanthia, these are so unusual that the genus should not be placed in the Mapanieae, not even in a separate subtribe, but in a new tribe, Syntrinemeae. Its differences from the Mapanieae are:

1. In the Mapanieae, each pseudospikelet is a visibly separate unit, even in those species of *Mapania* where they bunch together into a congested terminal inflorescence, and in *Chrysithrix* where the pseudospikelet is reduced to a single pseudanthium. In *Syntrinema* the pseudospikelets borne on a culm are united into a single dense spicate head in which the individual pseudospikelets cannot be distinguished without dissection.

2. The size and habit of the plant are completely different from almost all species of Mapanieae.

3. The glumellas are in the form of bristles, not laminas as in all Mapanieae.

4. Two lower, lateral, folded glumellas occur in all Mapanieae except *Chrysithrix*. In *Chorizandra* they occur but are not folded so strongly nor is the whole midvein ciliate (according to Clarke's drawing in Tab. CXIX). *Syntrinema* does not possess these lateral, longitudinally folded glumellas.

5. In the Mapanieae there is only one kind of pseudanthium, which is bisexual. In *Syntrinema* there are three kinds, one bisexual, one male or possibly neutral, and the third male.

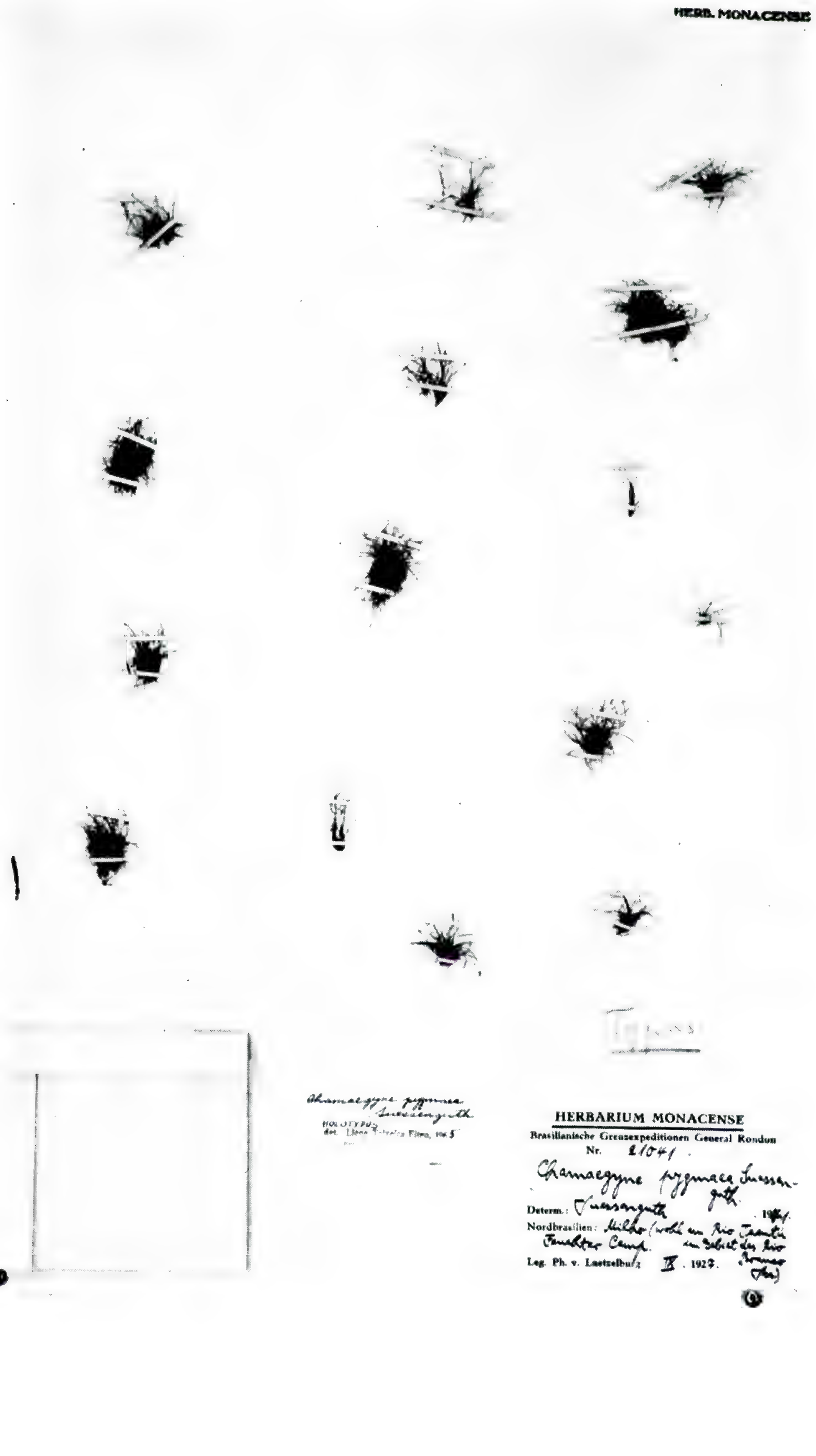
Syntrinemeae L. T. Eiten, trib. nov.

Inflorescentia capitulum unicum pseudospiculis spicata dispositis; quaeque pseudospicula prophyllo et bractea inferiore vacuis et ca. 9–10 pseudanthiis spicate dispositis in axillis bractearum glumiformium obsita; 2 pseudanthia inferiora bisexualia, quidque 3 floribus masculinis unistaminatis lateralibus in axillis glumellarum setiformium et flore femineo terminali (aut pseudoterminali?) cum pistilo unico et 3 glumellis setiformibus hypogynis; 2 pseudanthia sequentia masculina (neutra?), quidque 1–2 floribus masculinis lateralibus unistaminatis (aut staminodiis?) in axillis glumellarum setiformium; cetera pseudanthia quidque 3 floribus masculinis unistaminatis; in hoc pseudanthio 3 filamenta in columna connata et 3 antheris liberis, rachilla et glumellae setiformes non separate visibilis, aut carentes aut adsunt et cum columna filamentorum connatae.

A tribu Mapanieae differt: pseudospiculae in capitulis aggregatae; pseudanthia masculina ac bisexualia adsunt; glumellae setiformes. A tribu nova Micropapyreae differt: pseudospiculae in capitulis aggregatae; pseudanthia masculina ac bisexualia adsunt.

Type genus: *Syntrinema* Pfeiffer, Repert. Spec. Nov. Regni Veg. 21: 238. 1925.

I hereby designate the sheet of *Luetzelburg 15484*, deposited in the Botanische Staatssammlung München (M), as lectotype of *Syntrinema brasiliense* Radlk. & Pfeiffer because it is the only one of the three cited syntype collections marked on the sheet as "Typus." I exclude as part of the lectotype the fragments of *Chorizandra* in the envelope glued to this sheet.


HERB. MONACENSE
Chamaegyne pygmaea Suessenguth
HOLOTYPUS
HERBARIUM MONACENSE
Brasilianische Grenzexpeditionen General Rondon
Nr. 21041.
Chamaegyne pygmaea Suessenguth.
Determ.: Suessenguth 1934.
Nordbrasilien: Mühe (wohl am Rio Teantin
Leg. Ph. v. Luetzelburg III. 1927.

Chamaegyne pygmaea Süss.

(= *Eleocharis chamaegyne* L. T. Eiten)

Description of the holotype of *Chamaegyne pygmaea* Süss., Bot. Jahrb. Syst. 73: 114–115. 1943: Brasilia septentrionalis [Território de Roraima], Milho, prope Rio Tacutu, in ditione fluvii Rio Branco, in campo humido, Sep. 1927, *Luetzelburg 21041* (M).

The plant forms minute clumps (it is not known whether these were isolated or were pieces pulled out of a continuous mat) up to 3 cm tall (Fig. 22). The roots are abundant and vigorous in relation to the size of the plant. The mature culms are 5–25 mm long and 0.10–0.22 mm wide, triangular in cross section with each face depressed and forming an obtuse angle in its middle, light grayish green densely lined with purplish brown. At the base of each culm there is a triangular scalelike prophyll 1.2–3.5 mm long with two convergent veins (Fig. 23, a). Above the prophyll two leaf sheaths enclose the lower part of the culm; the lower sheath is external, 1.0–2.0 mm long, with a slightly wider apex of thin tissue and an oblique mouth (Fig. 29, b); the upper sheath is internal, 3.5–6.0 mm long, with a visibly wider or slightly inflated apex of thin tissue and an oblique mouth (Figs. 23, b; 29, c); this sheath is rose-purple, becoming lighter around the mouth. When young the culm is completely included in the lower sheath (Figs. 23, d; 28, d).

The spikelets are of two kinds: solitary and terminal at the culm apices, and sessile at the base of the clump between the culm bases. The spikelet at the culm apex is elliptic-oblong, flattened, (1.0–)1.5–1.6(–2.0) mm long and 0.2–0.3 mm wide. It has two subopposite, membranous, laterally folded glumelike bracts with the dorsal midvein greenish and streaked with purplish brown lines, and with the lateral portions hyaline with purple spots. Both of these laminas would usually be called glumes, but for reasons explained in the section on *Helonema*, I prefer to consider the lower one not part of the spikelet proper; it is therefore not to be called a glume but rather an associated scale. It surrounds the base of the upper lamina or true glume and never bears a flower. The true glume usually contains a male flower with 2–3 stamens (Figs. 30–34) or sometimes a bisexual flower consisting of a pistil and 1–2 stamens (Fig. 27). Rarely, the true glume is empty also.

When a culm does not have an apical spikelet, its apical meristem is covered by two scalelike subopposite bracts, the lower larger and surrounding the upper (Fig. 25). This lower bract is homologous with the associated scale on a culm tip bearing a spikelet; the upper bract is homologous with the lowest true glume, i.e., in 1-flowered spikelets such as in this species, with the single true glume. Sometimes the culm tip produces a vegetative shoot consisting of a whorllike short sympodial axis with a series of culms (Fig. 26). The first culm (Fig. 26, c)

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FIGURE 22. Holotype sheet of *Chamaegyne pygmaea* Süss. (= *Eleocharis chamaegyne* L. T. Eiten); *Luetzelburg 21041*; × 0.4. Each piece on this sheet was probably part of one mat. The following drawings of this species, Figs. 23–52, were made from plants of this sheet.

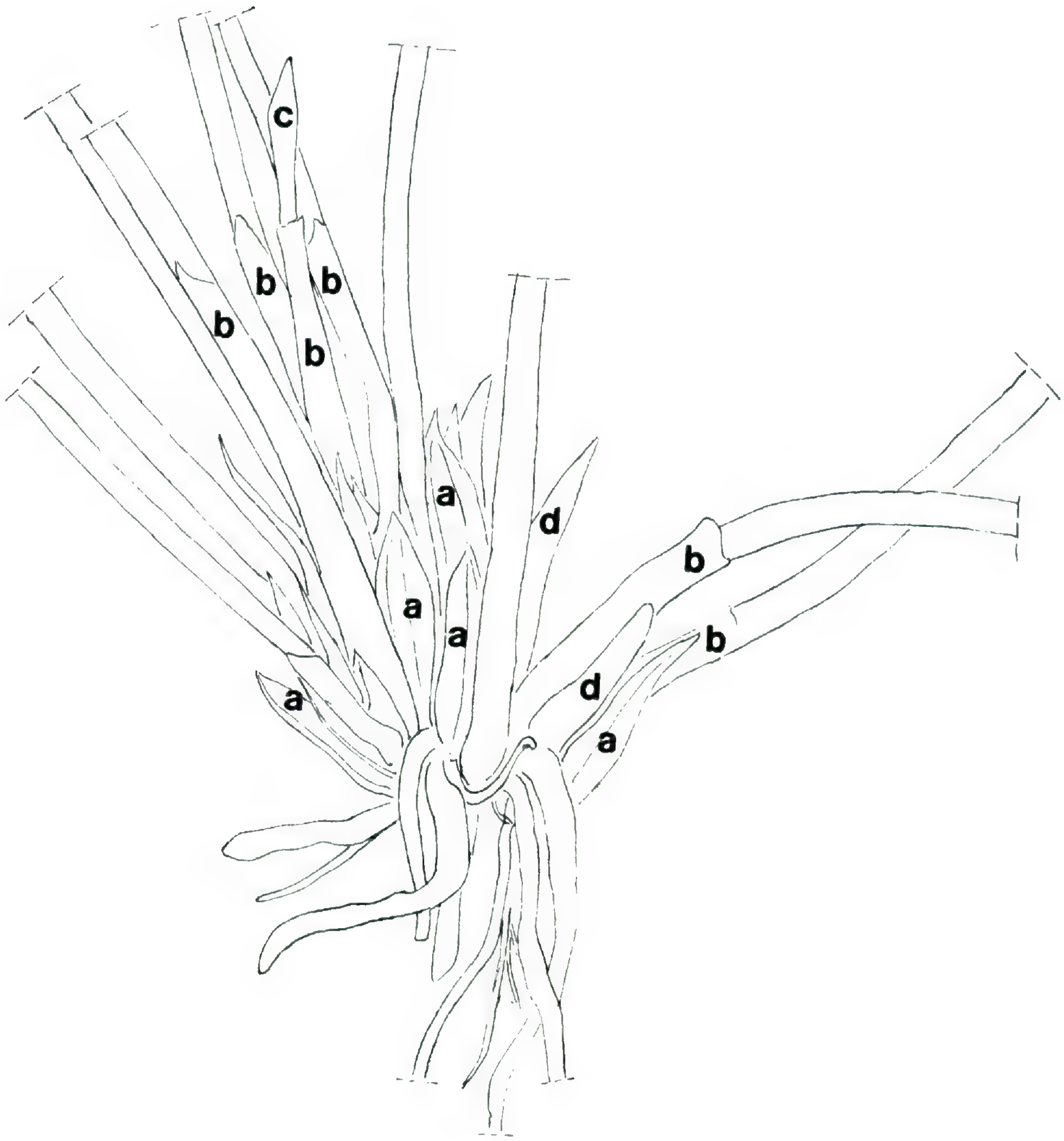
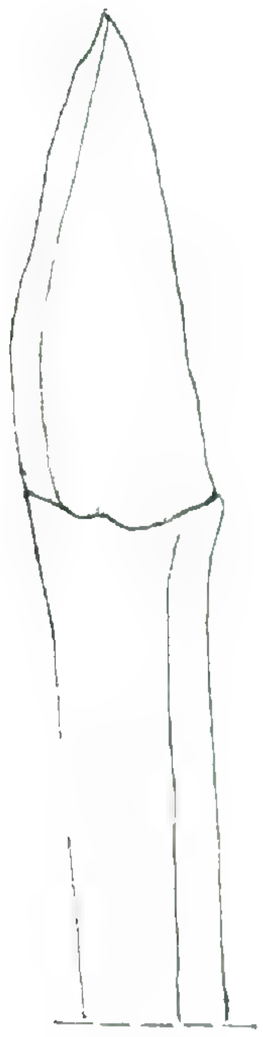


Figure 23. Base of clump without basal spikelets; × 23. a = prophylls; b = upper leaf sheaths; c = young culm with male spikelet; d = young culms still covered by their prophylls and sheaths.

of such a short shoot arises in the axil of the lower apical bract (Fig. 26, a). The second culm (Fig. 26, f) arises from the meristematic base of the first culm in the axil of one of the two leaf sheaths, penetrates the base of the sheath(s) and immediately emits a prophyll (Fig. 26, e). The third culm of the shoot arises from the base of the second culm and emits its prophyll, etc. A diagram of this branching is shown in Fig. 110.

The sessile spikelets at the base of the clump terminate very short axes which arise between the culms (Figs. 24, 35–38). This short axis has as its lowermost lateral organ a triangular prophyll with two convergent nerves (Figs. 37, a; 38, a; 40). Above the prophyll there are 1–2(–3)empty, wide, membranous scales with

FIGURE 24. Base of clump with basal spikelets; × 22. Note roots, base of culms (some with leaf sheaths visible), young basal spikelets with stigmas projecting from between glumes, and basal spikelets with mature fruits.



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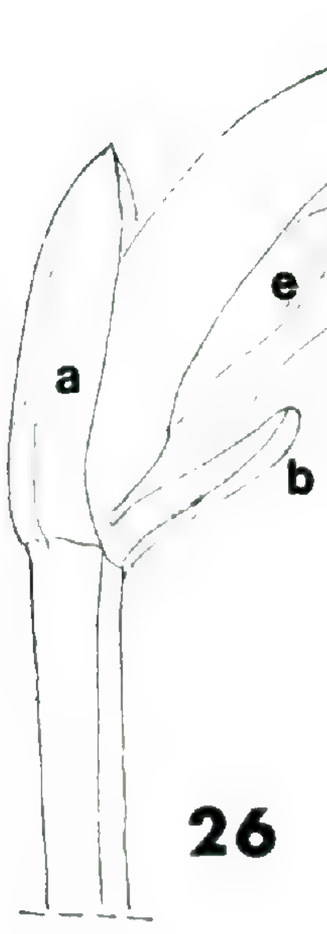

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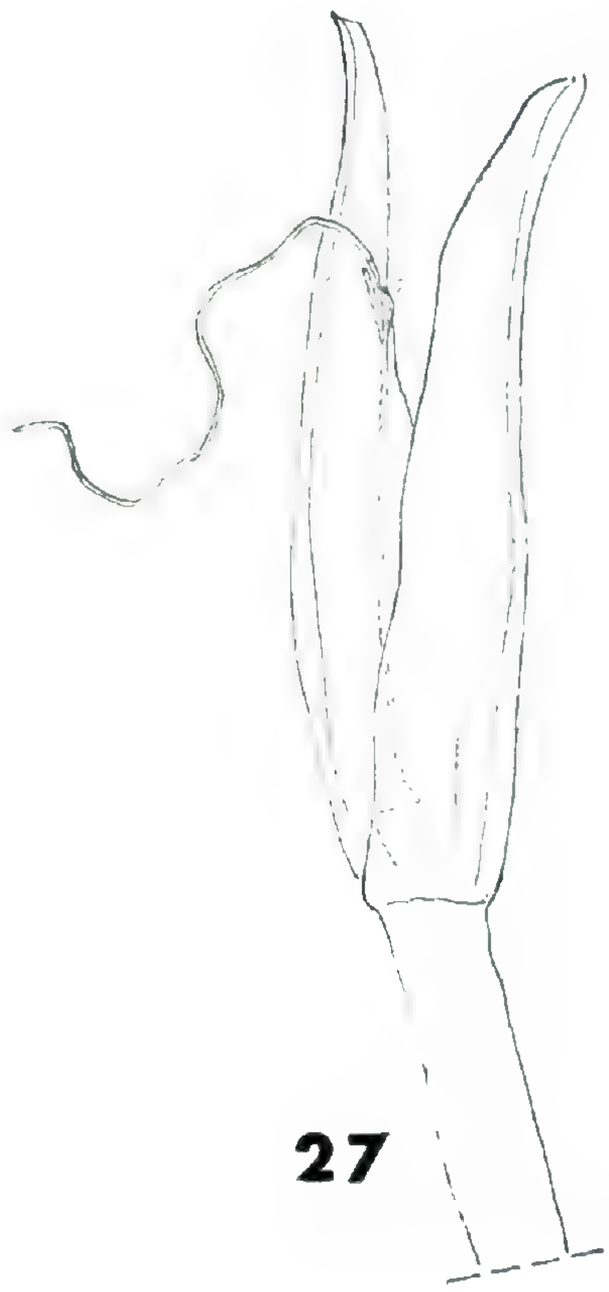

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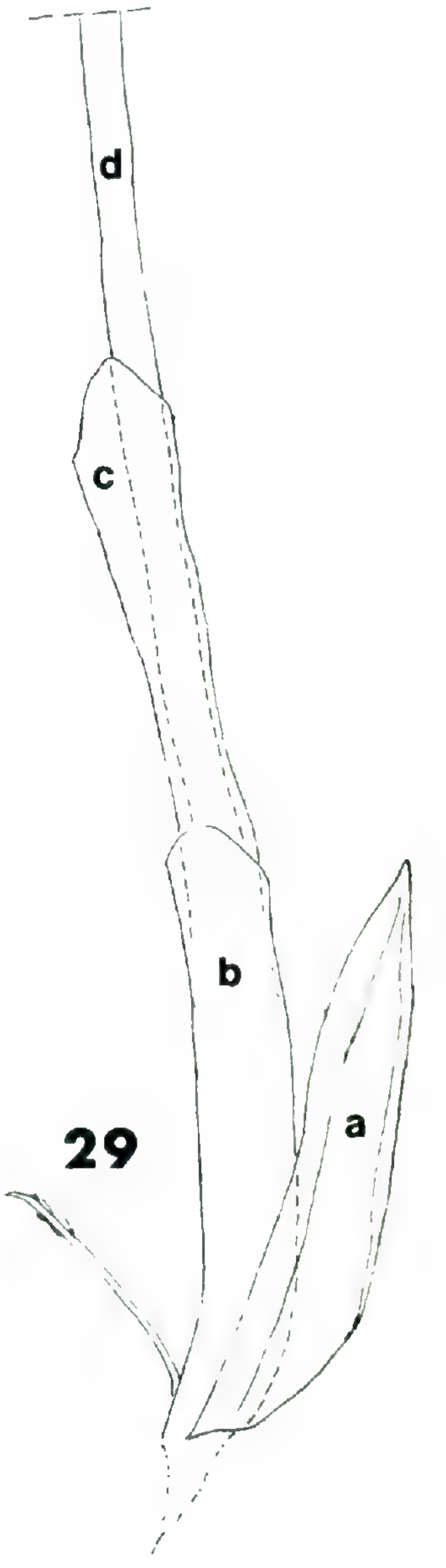

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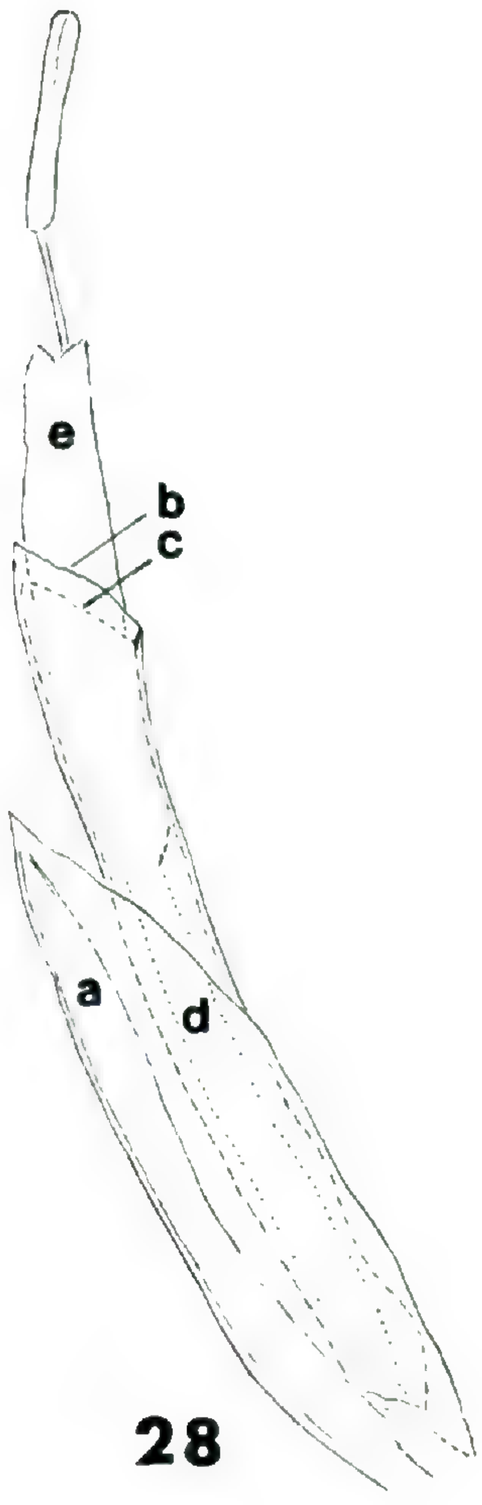

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an obtuse or rounded apex and with one midvein which is slightly visible or not visible (Figs. 35–37, b, c, d; 38, b; 39). At the tip of the axis are two longer subopposite laminas. The lower is the associated scale (Figs. 35–37, e; 38, c; 41) and the upper is the true glume (Figs. 35–37, f; 38, d; 42). The associated scale and the glume are lanceolate, membranous, 1.8–2.8 mm long and with a purple median stripe on the dorsal surface. The associated scale is always empty and surrounds the base of the glume, which contains the flower. Besides these parts, the short axis sometimes has another wide short scale just above the prophyll; in the axil of this scale there is a stem rudiment with a basal ligule (Fig. 37, b). In other short axes, this extra scale is lacking but in the axil of the prophyll there is a vegetative formation consisting of two tubular membranes like the fingers of a glove, the lower containing the upper and both covering a meristematic point (Fig. 43, b).

In the basal spikelets the flowers are female (Figs. 43–44) or bisexual (Figs. 45–48); in the latter, 1–2 stamens accompany the pistil. The stamens have hyaline filaments and golden-yellow anthers. The pistil is trigonous with a separately marked-off stylebase, a trigonous style, and three stigmatic branches with short transparent hairs (Fig. 49).

The mature achene has a globose-trigonous body 0.7–0.9 mm tall (not counting the stylebase) and 0.6–0.7 mm wide; the surface is cancellate (with large rectangular depressions in vertical files) and dull ivory-white. The stylebase is pyramidal, 0.15–0.25 mm tall, 0.3 mm wide, and dull dark brown (Figs. 50–52).

There exists a short note by Süssenguth (1952) on an unpublished anatomical investigation of *Chamaegyne* made by L. Bittl which is preserved in the Munich herbarium.

Süssenguth (1943) thought that *Luetzelburg 21041* is related to *Eleocharis* by its similarity in habit, form of stylebase, and presence of leaf sheaths at the

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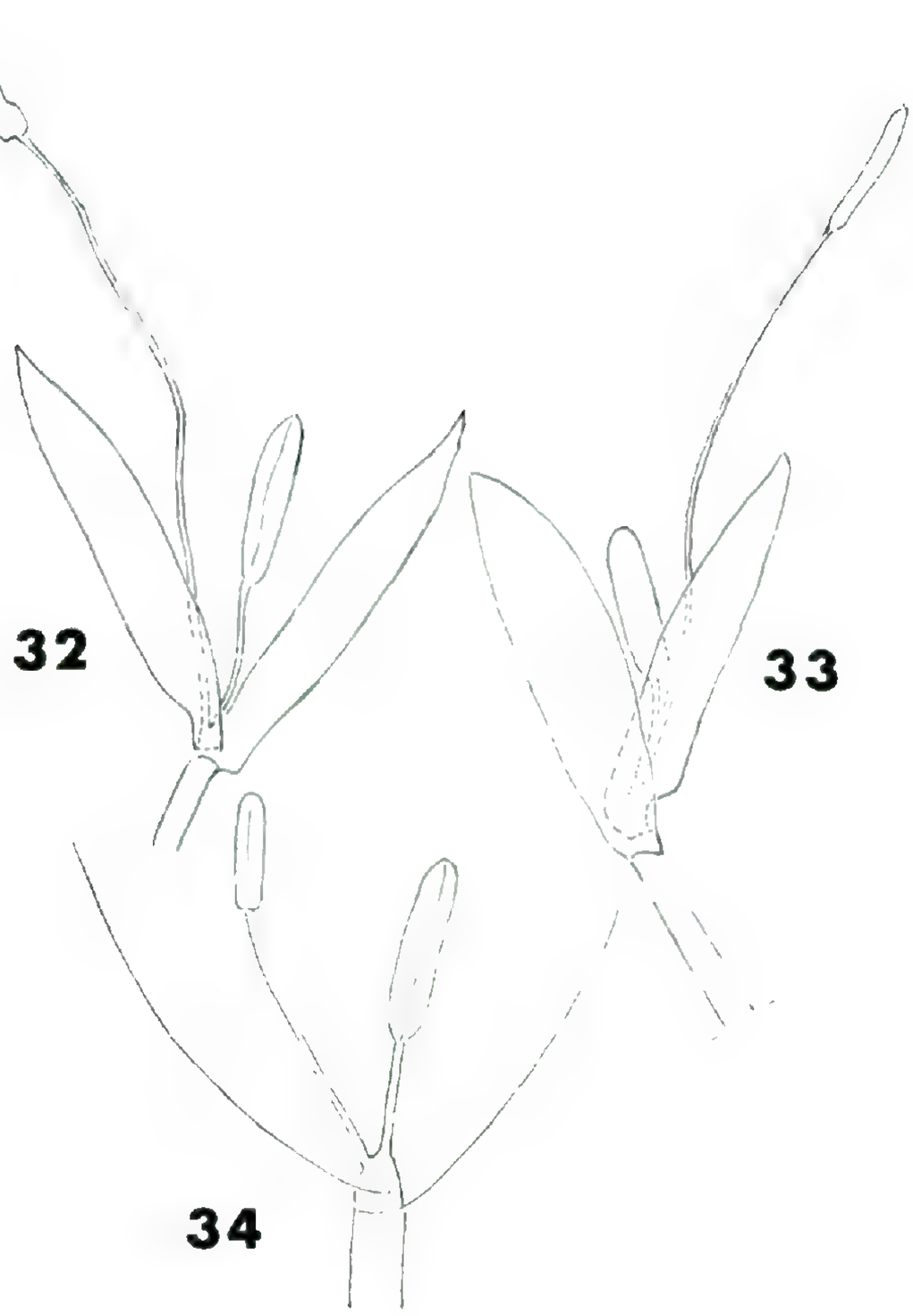
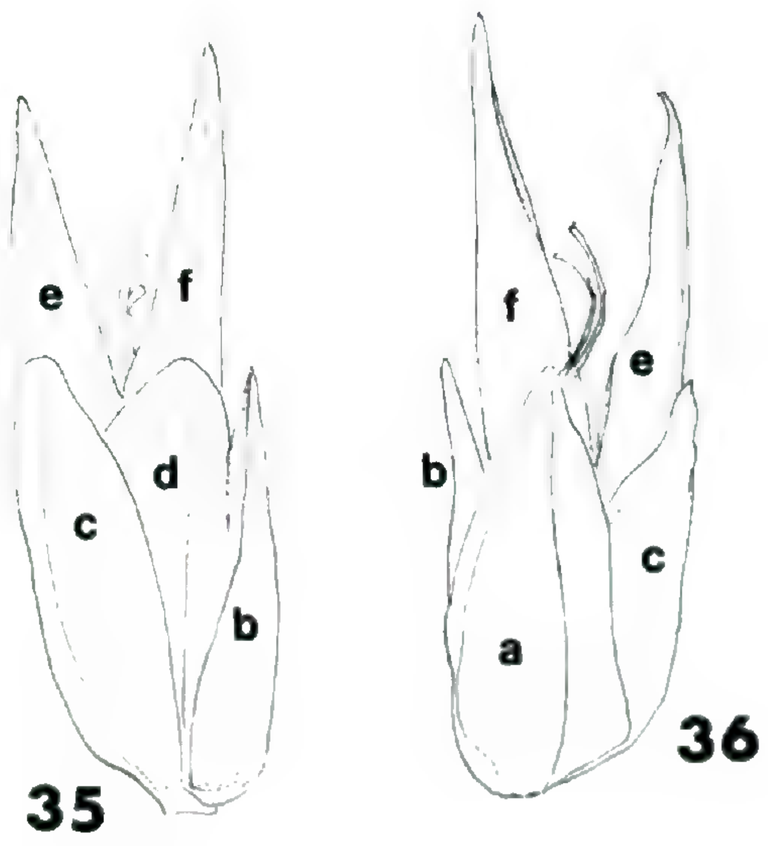
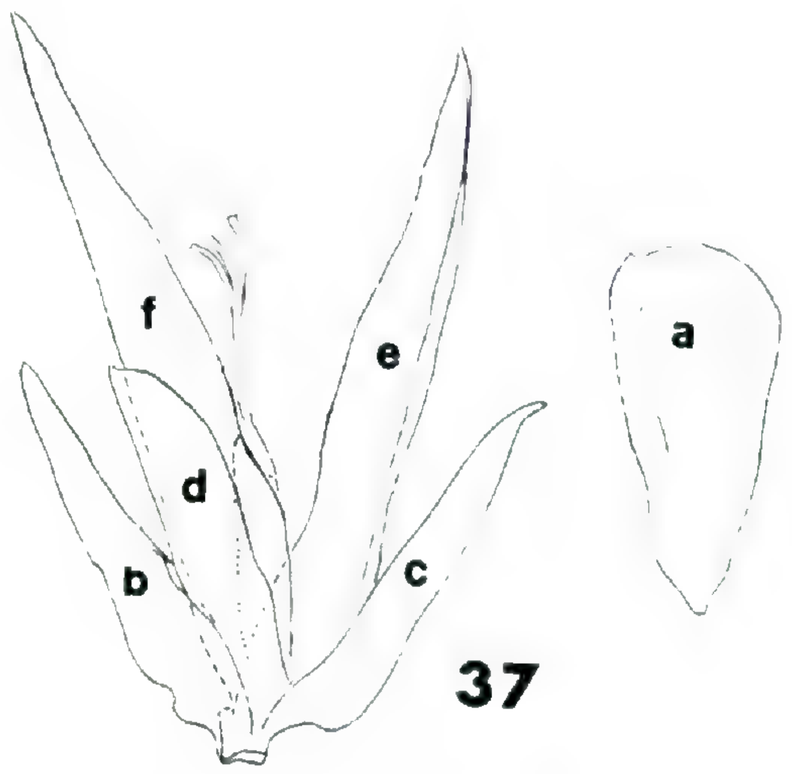
FIGURES 25–31.—25. Culm tip; × 66. Lower enrolled bract with margin visible. This bract totally covers the upper bract; both surround the meristematic culm tip.—26. Culm tip with young shoot; × 27. a = lower external bract at base of shoot; b = upper external bract at base of shoot; c = young culm arising from axil of bract a; d = upper or internal leaf sheath (the lower was not visible and is not shown); e = prophyll at base of the very young culm f; f = young culm still covered by its leaf sheaths. The lower bract, a, is homologous with the associated scale on a culm tip bearing a spikelet; the upper bract, b, is homologous with the single true glume of a spikelet.—27. Culm tip with terminal spikelet; × 43. Associated scale on right, glume subtending bisexual flower on left; filament from which anther has fallen extends to left.—28. Very young culm; × 13.6. a = prophyll; b = lower leaf sheath; c = upper leaf sheath (shown in dashed outline) still completely within lower sheath; d = culm (shown in dotted outline) still enclosed in its leaf sheaths; e = male spikelet. Even though the culm itself is just starting to lengthen, the filament of its spikelet flower is lengthening preparatory to anthesis.—29. Base of culm which bears a male spikelet; × 13.6. a = prophyll with two convergent veins; b = lower leaf sheath; c = upper leaf sheath; d = lower part of culm. In Figs. 28 and 29 the prophyll at the base of the axis is the prophyll of that axis and not the prophyll of a new axis that arises from it. This is because the ventral surface of the prophyll is turned towards the axis and not addorsed to it.—30. Culm-tip spikelet with male flower with three stamens, one still with its anther; × 16.5.—31. Semidiagrammatic representation of spikelet in Fig. 30. The apparently terminal male flower is really lateral (i.e., pseudoterminal) and arises in the axil of the glume (the upper lamina).







FIGURES 32–37.—32–33. Two views of a male spikelet at a culm tip; × 12.5. Note the associated scale and the glume arising at different levels and the flower with two stamens. The lengthening of the filaments is not synchronous.—34. Semidiagrammatic representation of this spikelet showing the pseudoterminal position of the flower.—35–36. Short axis with basal spikelet; × 28. Two views with parts in natural position. a = prophyll; b–d = scales; e = associated scale; f = glume with female flower (pistil).—37. Same spikelet with parts spread out; × 28. The small body in the axil of scale b is a branch from the rachilla which bears a ligule and meristematic rudiment not visible in this drawing.

base of the culms. However, he kept this species out of *Eleocharis* for two reasons: lack of a "perianth," i.e., bristles, and because the flowers are solitary (Einzelblüten), that is, not in spikelets. By Süssenguth's definition, a spikelet has to have more than one flower. Therefore, he set up the new genus *Chamaegyne*. But these two reasons are not really valid. In *Eleocharis*, bristles are not always present. There are species in which some individual plants have bristles with the achenes and others not. Frequently, on the same plant, young flowers do not show bristles while mature flowers and achenes show them. As for the "solitary flowers," that is, 1-flowered spikelets, these also occur in *Eleocharis*. There are species such as *E. minima* Kunth, whose apical spikelets usually have many to few flowers, but sometimes, even in good growing conditions, produce some 1-flowered spikelets, with only an associated scale ("empty glume") and the one true glume which subtends and encloses the flower. The spikelets of *E.*

TABLE 1. Comparison of the lateral organs on the culm and short axis of *Eleocharis chamaegyne* L. T. Eiten.

Culm	Short Axis
1 prophyll (scale with 2 convergent veins)	1 prophyll (scale with 2 convergent veins)
2 sheaths (with a midvein slightly or not visible)	1–2(–3) short wide scales (with a midvein slightly or not visible)
1 empty glumelike lanceolate associated scale	1 empty glumelike lanceolate associated scale
1 lanceolate glume with flower (rarely empty)	1 lanceolate glume with flower
male flower (rarely bisexual)	bisexual flower (sometimes female)

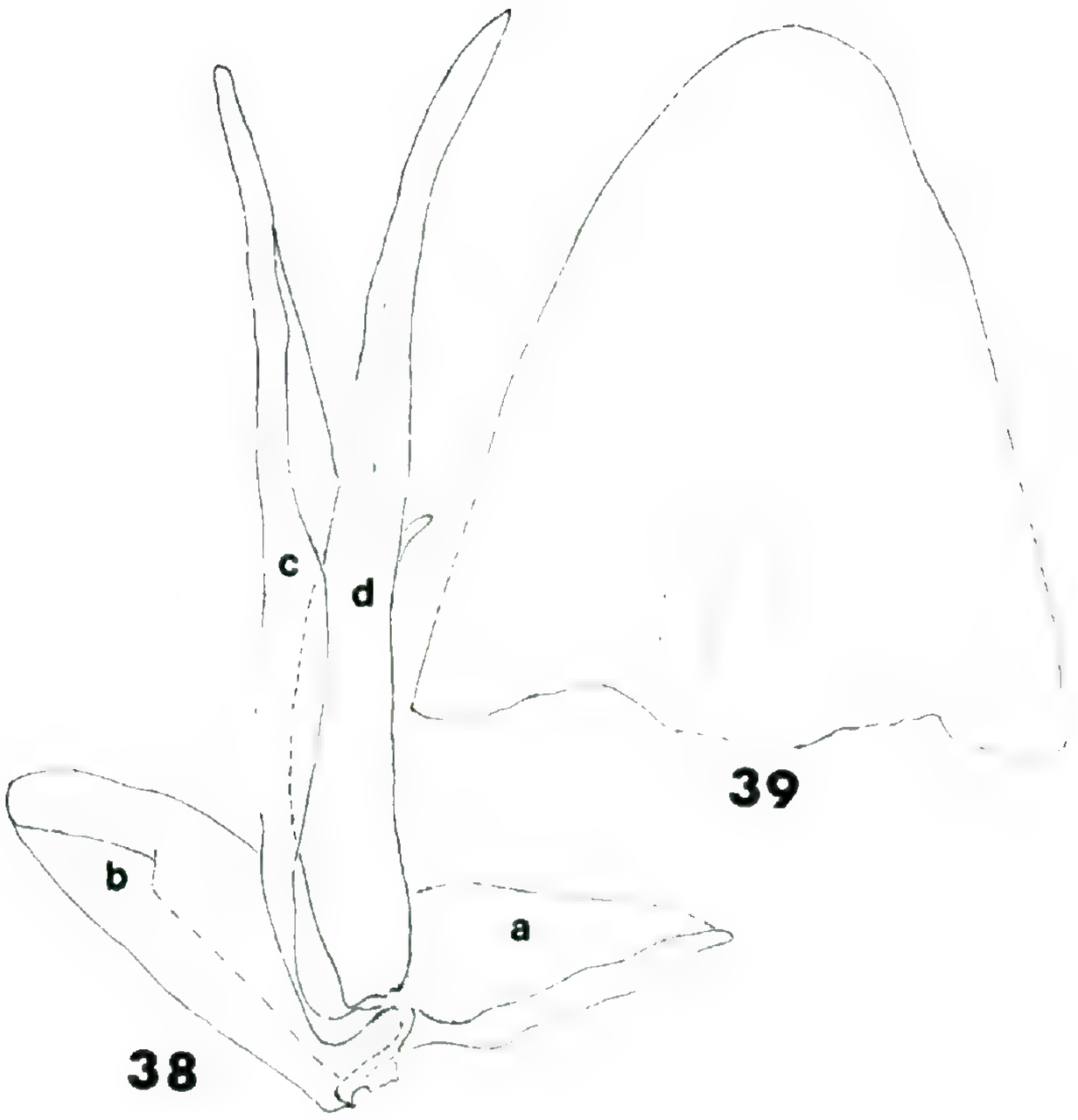
capillacea Kunth are 1-flowered with an associated scale and the glume which bears the flower. Rarely, in this species one can find spikelets with two or even with three flowers. In *E. naumanniana* Boeck. the apical spikelets are always 1-flowered, with an associated scale and a flower-bearing glume.

When Süssenguth (1943) described *Chamaegyne*, he mentioned that the plant has a rosette of leaves, that is, leaf blades. He wrote, "Blüten sitzen einzeln zwischen den Blättchen an der Erde." He stated that four leaves surround the pistil in the basal spikelets and that they are "foliis normalibus nec bracteosis nec glumaceis." The presence in *Chamaegyne* of "normal leaves," that is, leaves with true blades, would be a sufficient reason for excluding it from *Eleocharis* but, strangely, Süssenguth does not mention this character in his argument for separation. However, the only organs to which he can be referring are the glume, the associated scale and the usual two short scales of the short axis. He describes the "leaves" as being "Cr. 2 mm longe, lanceolata, acuta, tenerrima, integra, glabra, aliquando subfalcata;" these are exactly the characteristics of the associated scale and glume of the basal spikelets. The drawing of *Chamaegyne* given by Süssenguth (1943: Abb. 1) shows a pistil and a fruit between laminas which are undoubtedly these organs. Since the mature fruits fall from the basal spikelets, leaving their glumes empty, these empty associated scales and glumes at the base of the clumps are the remaining "leaves" which he shows in his drawing not associated with pistils or fruits. The prophyll and 1–3 scales which also occur below the glume and associated scale and are only a third to a half as long are not shown in Süssenguth's drawing. These scales and glumes are not normal leaves but rather opened-out and transformed leaf sheaths.

There exists a homology between the lateral organs on the culms and those on the short axes which bear the basal spikelets (Table 1).

The spikelets of this species should be defined so as to include only the uppermost lamina, that is, the true glume, and the flower in its axil. In this way, the definition is uniform for spikelets on culm tips and on the short axes, since the number of short scales between the prophyll and the associated long scale varies.

Although usually I have found male 1-flowered spikelets on the tip of developed culms, sometimes the flower was bisexual and mature. Süssenguth also



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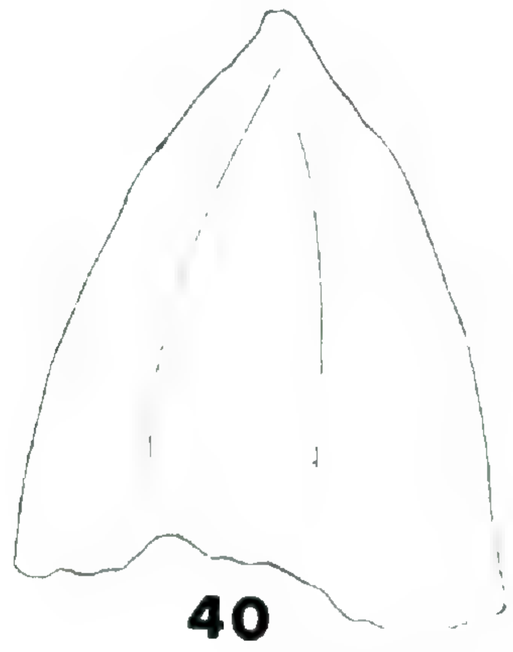

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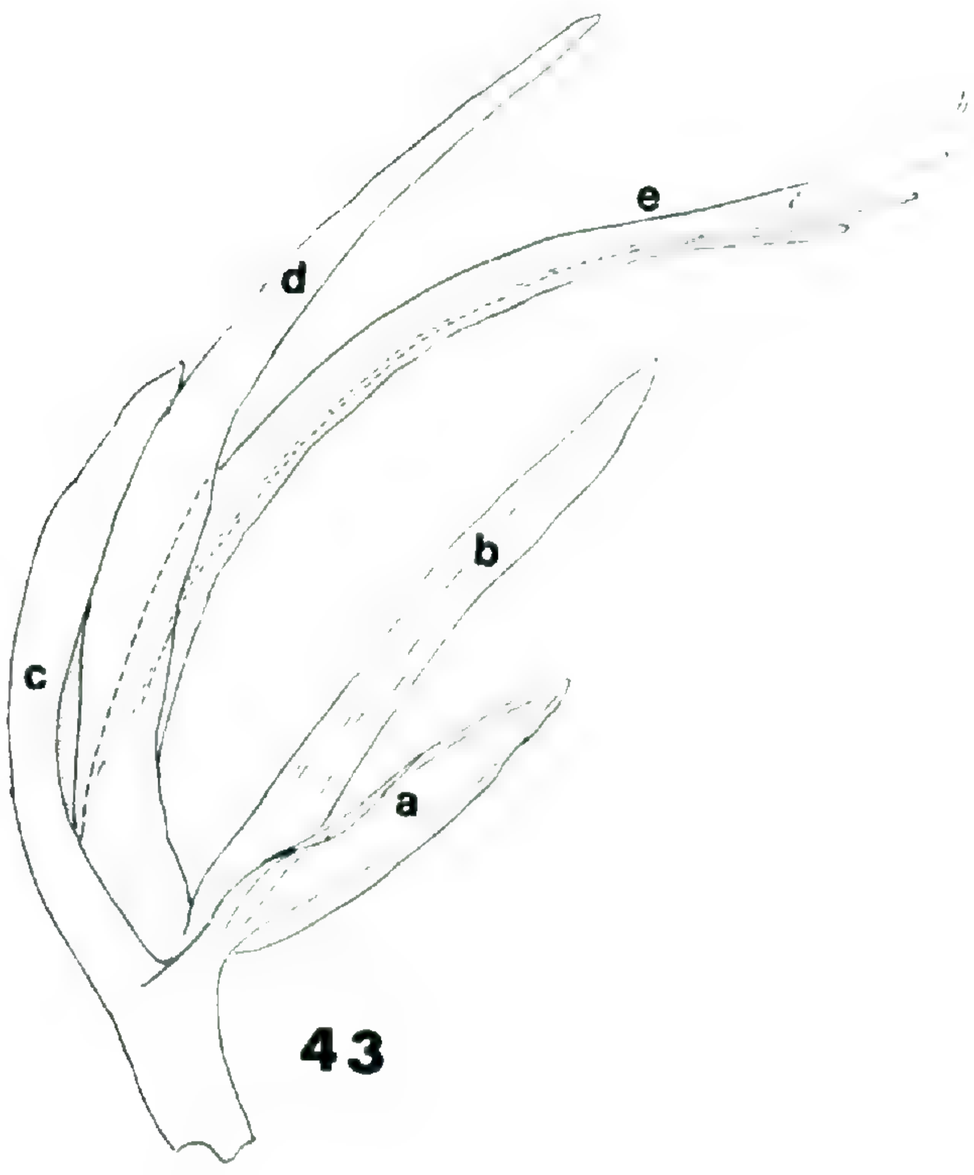

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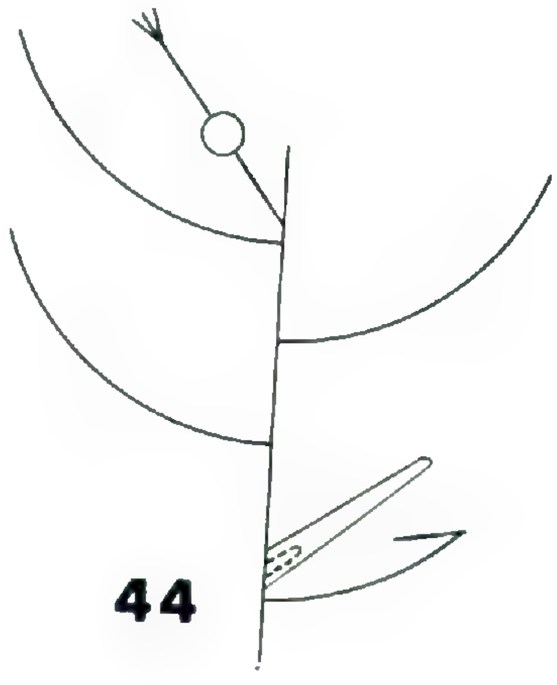

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FIGURES 38–44.—38. Short axis with basal spikelet with bisexual flower; × 40. a = prophyll; b = scale; c = associated scale; d = glume with flower. The prophyll and scale have been pulled down; part of the near side of the scale has been cut away to expose base of associated scale and glume.—39. Scale b flattened out, showing dorsal surface; × 60.—40.

found a young bisexual flower in a culm tip spikelet that had not yet grown out of its sheath, but he thought it was a teratological phenomenon ("aliquando in folio vaginali tubuloso, in quo scapis floris masculi expectatur, ovarium cum stylo etc., reperitur, quod autem nunquam maturescit et casum teratologicum offerre videtur"). The presence of bisexual flowers in the culm tip spikelets in *Chamaegyne* relates the species more closely to *Eleocharis* in which this is the usual condition.

The flowers which Süssenguth considered pseudobisexual because they possess stamens with twisted anthers ("mit einer verkummerten Anthere") are really ordinary bisexual flowers. The anthers become twisted in anthesis as is common in all Cyperaceae.

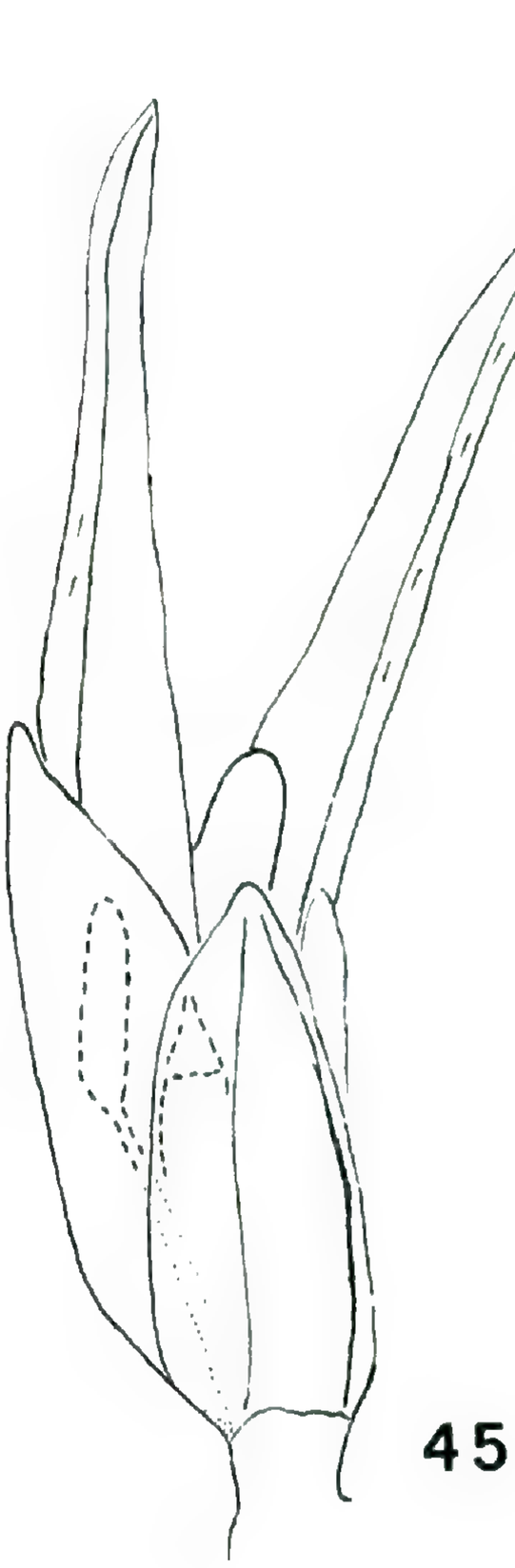
From this exposition there remains no character that really distinguishes *Chamaegyne* from *Eleocharis*. I am convinced that the material of *Chamaegyne* belongs to a species of *Eleocharis* series *Tenuissimae*. Svenson (1937: 212) says: "In the dwarf species of the *Tenuissimae*, and nowhere else in the genus, sessile basal spikelets are of frequent occurrence. These are found at the culm-bases, often so abundantly as to form scaly bulblike masses. Each spikelet is 1-flowered, developing a single achene which is usually a little larger than the achenes produced in the normal spikelets. . . . Similar basal spikelets have been described by Chermezon in three Madagascar species of *Scirpus*, ... Such spikelets, according to Chermezon, are perhaps the result of alternate immersion and emersion."

Within the series *Tenuissimae*, *Chamaegyne* seems to be related to *Eleocharis minima*. Svenson (1937) gives a drawing of the basal spikelets of this species in his Plate 465, Fig. 8, which is very similar to my drawing, Fig. 24, which was made before I noticed the relationship between these two species. Also, the apex of the leaf sheaths of both species is somewhat widened or even a little inflated.

Despite these similarities, I believe *Chamaegyne* is a different species from *E. minima*. The principal difference is in the achene. *Eleocharis minima* has ellipsoidal-trigonous to obovoid-trigonous fruits which are 0.75–1.0 mm long (with stylebase), whitish to pale brown or olive, the surface marked with fine shallowly depressed rectangles with the long axis vertical. The achene of *Chamaegyne* is globose-trigonous, 0.85–1.1 mm long, dull ivory-white, the surface strongly cancellate with deep wide rectangles with the long axis horizontal (Fig. 52). The stylebase in *Chamaegyne* falls within the range of variation which this structure presents in *E. minima*.

In view of the difference in the fruits, organs of primary importance in separating species in *Eleocharis*, I consider *Chamaegyne pygmaea* as a new species. Its formal transfer was made in Eiten (1970: 273), where it was called *Eleocharis*

Prophyll flattened out, showing dorsal surface with two convergent veins; × 60.—41. Associated scale of a basal spikelet.—42. Glume. Both are flattened out and in dorsal view; × 40. Note vertical median thicker part and small elongated purplish brown streaks.—43. Short axis with basal female spikelet, the parts somewhat spread out; × 25. a = prophyll; b = tubular membrane (leaf sheath?) covering a meristematic rudiment (new culm?); c = empty short scale; d = empty associated scale; e = glume with pistil inside.—44. Branching pattern of this short axis.



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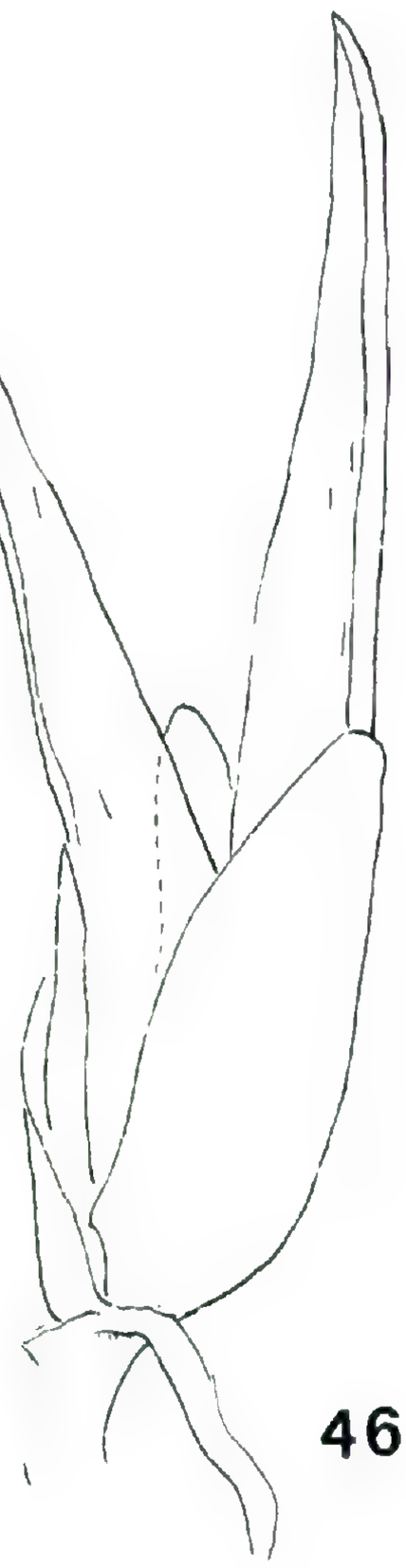

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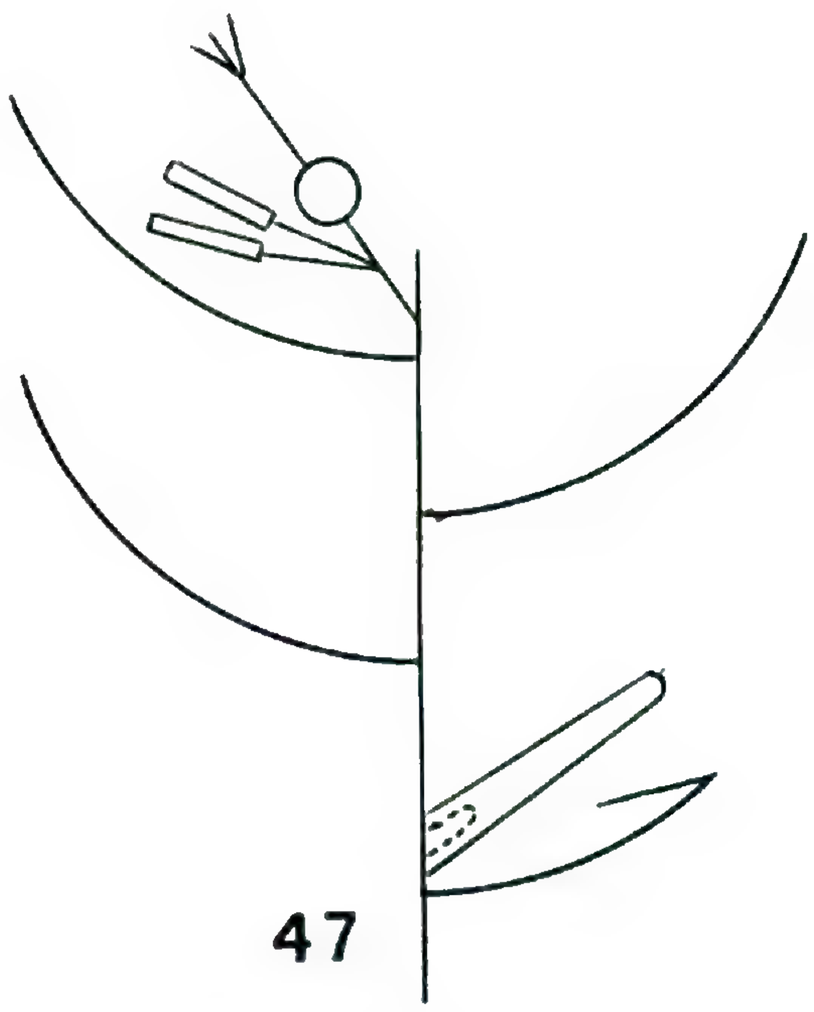

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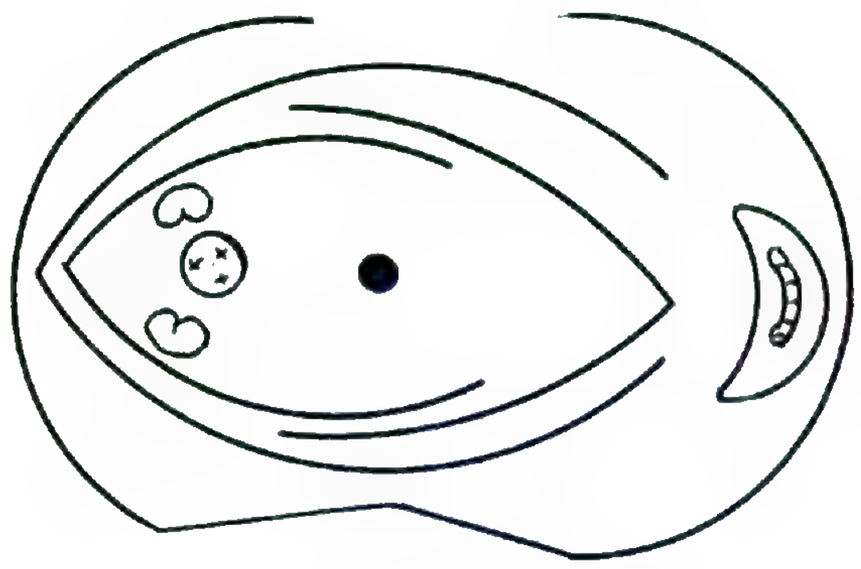

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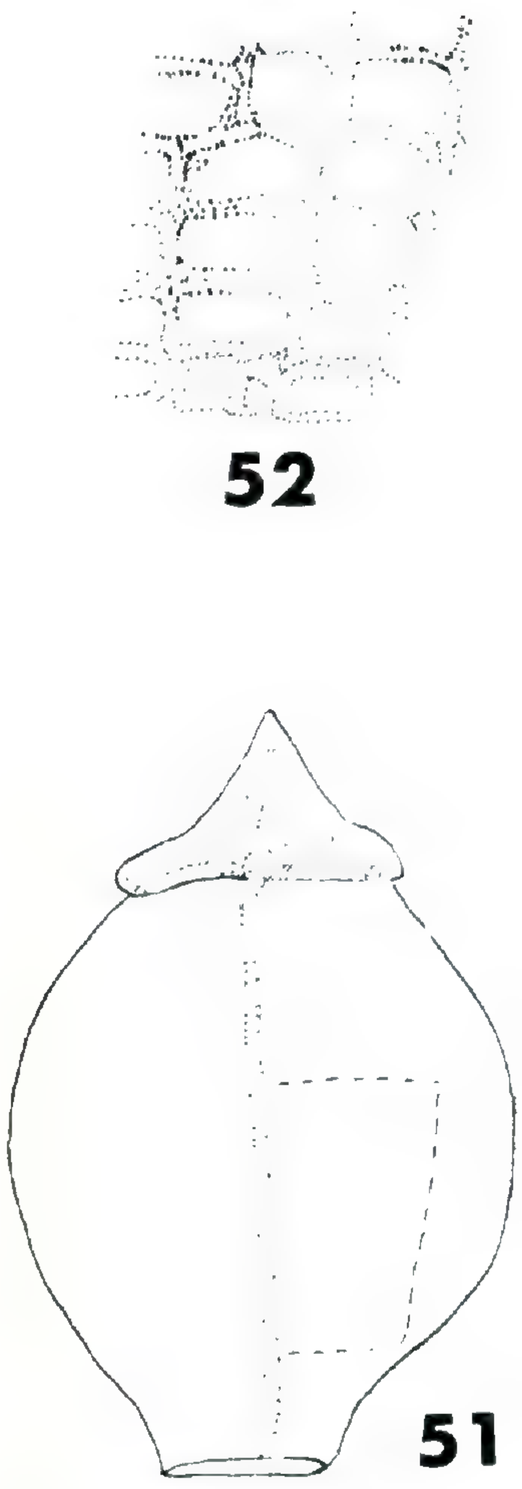
FIGURES 45–48.—45–46. Two views of short axis with basal spikelet; × 38. Note prophyll, single short scale, long associated scale and glume. The tubular membrane in the axil of the prophyll is also shown. One of the stamens and the pistil in dotted outline is shown.—47. Branching pattern.—48. Floral diagram of this short axis.



FIGURES 49–52.—49. Flower from a basal spikelet; × 49. Young stamen with filament which has not yet elongated, and anther before anthesis. The oblong-trigonous ovary has a differentiated style base, trigonous style, and three stigmatic branches with short hairs.—50. Achene in basal spikelet between its associated scale and glume with remains of stamens; × 30.—51. Mature achene with conical stylebase; × 48.—52. Detail of the rectangular area in Fig. 51, showing cancellate surface; × 115.

pygmaea (Süss.) L. T. Eiten. Since there was a previously published *Eleocharis pygmaea* (Torrey, 1836: 313), it was renamed *Eleocharis chamaegyne* L. T. Eiten (Eiten, 1972).

Since *Chamaegyne* is therefore considered a species of *Eleocharis* and is obviously a reduced form of it, the single flower in its spikelet is not terminal as it appears but is pseudoterminal, that is, really lateral in the axil of its glume as are all flowers in *Eleocharis*.

Collections of other species examined (all det. L. T. Eiten) in connection with this study of *Chamaegyne*:

Eleocharis capillacea Kunth

BRAZIL: AMAZONAS: Manaus, margem do Igarapé do Cachoeira Alta, 10 Aug. 1955, *Chagas s.n.* (INPA, UB). GOIÁS: *Glaziou* 22328, ex herb. Schwacke (RB). DISTRITO FEDERAL: Catetinho, perto de Brasília, 25 May 1965, *Sucre* 320 (UB). SÃO PAULO: São Paulo, Butantan,

5 Sep. 1917, *Hoehne s.n.* (SP). Mun. de Mogi-Mirim, 23 May 1927, *Hoehne 25190* (SP). Mun. de Mogi-Guaçu, Fazenda Campininha, 21 Apr. 1960, *Eiten & Eiten 1950-B* (SP). PARANÁ: Ponta Grossa, 15 Dec. 1903, *Dusén 2707* (R).

Eleocharis naumanniana Boeck.

LIBERIA. MONTSERRADO CO.: Bushrod Island, 19 Aug. 1949, *Baldwin Jr. 13021* (US). Ca. 20 mi E of Monrovia, 20 Aug. 1949, *Baldwin Jr. 13049 a & b* (US).

Eleocharis minima Kunth

Cited at the end of the section on *Helonema*.

HELONEMA ESTRELLENSE Süss.

(= *Eleocharis minima* Kunth)

Description of the syntypes of *Helonema estrellense* Süss., Bot. Jahrb. Syst. 73: 118–119. 1943: Staat Rio de Janeiro, Serra Estrella, in Rio Gongojoco, Oct. 1916, *Luetzelburg 14062* (M). Staat Rio de Janeiro, Serra dos Órgãos, Grota do Inferno, Wasserfall, an Granit im Wasser, Jan. 1916, *Luetzelburg 14027* (M).

The plant is delicate with capillary culms and a filamentous flaccid habit, forming numerous verticillate shoots (Figs. 53–54). The largest piece found was 25 cm long and had two orders of shoots. The shoots form on the apices of the culms (Figs. 60–61), and appear to arise from between two scalelike basal bracts. The lower of these external basal bracts of a shoot continues in the direction of the culm just below it and is 0.8–1.2 mm long and 0.5 mm wide (Fig. 66); the upper external basal bract is 0.4–0.8 mm long and 0.3–0.4 mm wide. Both bracts have a wide green stripe along the dorsal midvein and relatively narrow membranous sides. A shoot has 3–8 culms 7–10 cm long; each culm is associated with a bract at its base which is generally membranous. These bracts are often missing either because they possibly have not developed, or more probably, because they have decayed. They probably are prophylls.

Each culm has two basal tubular leaf sheaths which are made of extremely thin, more or less transparent tissue; the outer sheath is very much shorter than the inner (Fig. 67). Sometimes the sheaths are found with only short fragments of culm inside or they are completely empty. When empty, the sheaths in dry pressed material appear to be narrow, flat, thin leaf blades since the outer sheath is difficult to see and the walls of the inner sheath are glued to each other to form a flat lamina. Some culms (1–3) of a shoot bear new shoots at their tips made of 3–6 culms 1–3 cm long. At the base of the culms in a shoot, roots are commonly found. When a culm apex has neither a shoot nor a spikelet, the terminal meristem is covered by two small scalelike bracts; the lower is enrolled and oriented so as to continue the line of the culm; it grows beyond and encloses the smaller upper bract (Fig. 65). (In the fresh topotype material shown in Figs. 74–75, the two terminal bracts lie side by side.)

Vegetative multiplication by shoot formation at the culm tips and subsequent breaking of the older lower culms is the main method of reproduction of this plant when submersed. Spikelets form rarely, are very small and not evident. In the syntype material, the associated scale next to a spikelet (usually called the lowest glume by authors speaking about *Eleocharis*) always has a meristematic shoot of 1–2 culms in its axil (Figs. 55–57, 68, 70), or the shoot has grown into a young stage (Fig. 67), or it is well developed (Figs. 58, 63–64). In these shoots,

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FIGURE 53. Syntype sheet of *Helonema estrellense* Süss. (= *Eleocharis minima* Kunth, extreme aquatic phase); *Luetzelburg 14027*; ×0.4. Figures 60–62 were made from material of this collection. The name shown in the annotation slip has since been changed.

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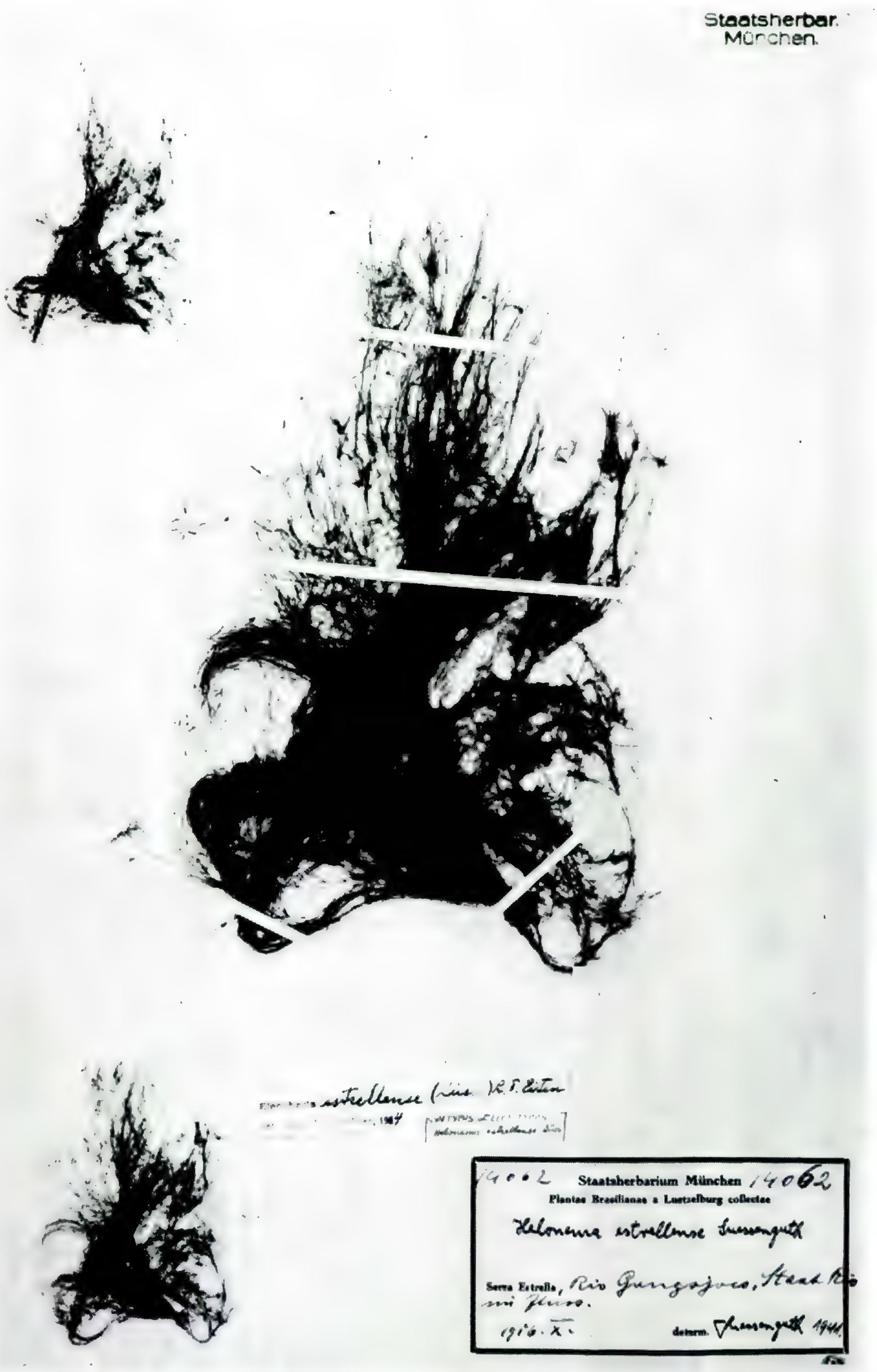

FIGURE 54. Lectotype sheet of *Helonema estrellense* Süss.; *Luetzelburg 14062*; × 0.4. Figures 55–59, 63–71 were made from material of this collection.

each culm arises from the base of a previously formed culm (branching pattern shown in Fig. 110). As in the basal shoots, a lamina is found associated with the base of some (Fig. 60) or all (Fig. 61) of the culms of a shoot. It is difficult to tell if these are prophylls, such as usually occur in *Eleocharis* clumps and culm tip shoots, or are opened-out lower leaf sheaths. Often no such scales are found among the culm bases (Figs. 58, 63) but whether they did not form in these cases, or formed and then decayed in the water, is difficult to tell from this material.

The spikelets are elliptical or oblong, flattened, 2.3 mm long and 0.6 mm wide. I exclude the associated scale ("lowest glume" of authors) and its axillary shoot

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FIGURES 55–62. Spikelets, flowers, and shoots from the syntypes.—55. Spikelet with associated scale and four glumes; × 18.—56–57. Spikelets with associated scale and two glumes; × 18. Note tendency for distichous arrangement in these spikelets with a low number of glumes.—58. Culm apex showing association of spikelet and shoot; × 36. The shoot has two developed culms and a young one. The small projection at base of the left culm is a scar left by the associated scale. The prophylls of the second and third culms are not shown; they probably had decayed in the water. The lower leaf sheaths were not visible and so were not drawn.—59. Young bisexual flower taken from spikelet of Fig. 58; × 36. Note absence of bristles.—60. Base of shoot at culm apex; × 30. There is no associated spikelet here. Note the two external bracts at the base of the shoot, the lower, a, (next to root) and the smaller upper one, b. (The two vertical lines in a are the borders of a thickened middle portion that contains the midvein.) The shoot has four developed culms and a wide basal lamina, d, associated with one of the culms. The young culm, c, is still covered by its hood of leaf sheaths. The lower external bract of the shoot, a, subtends the oldest culm; the other culms arise successively from the meristematic base of a previous culm in the axil of the outer leaf sheath. The upper external bract, b, although at the base of the whorl, does not subtend any of the culms.—61. Shoot at culm apex, not associated with spikelet; × 30. The base of one of the culms of the shoot emits a root which leads off to the left. The shoot has two external bracts, a and b. The first culm, c, is developed and is associated with the large lamina, d, which is its lower leaf sheath split and spread out. The second culm, e, also developed, is associated with the lamina, f; the young third culm, h, is still contained in the hood of a leaf sheath, and associated with the lamina, g. Laminas f and g are probably also split and opened out lower leaf sheaths.—62. Diagram of cross section of shoot of Fig. 61. This shows the assumption that the laminas f and g of Fig. 61 are opened out lower leaf sheaths and that the prophylls belonging to the second and third culms of the shoot have rotted away and so are not shown. The shaded circles are culms and the circles around them represent their upper leaf sheath.

FIGURES 63–69.—63. Shoot of three culms at a culm tip, associated with a spikelet; × 40. The associated scale, the prophylls, and the leaf sheaths had decomposed.—64. Semidiagrammatic representation of the spikelet in Fig. 63, showing rachilla, glumes, and flowers. In the lower flower, the ovary and the base of the two filaments had fused, forming the thick body shown.—65. Apex of a culm which does not bear a shoot or a spikelet; × 40. The meristematic culm tip is covered by two scalelike bracts; the lower is larger and enrolled and covers the upper.—66. Lower of the two external bracts at the base of a culm-tip shoot, spread out, showing thick median portion; × 40.—67. Culm tip with shoot and spikelet; × 40. Shoot consisting of associated scale (equivalent to lower external bract) and two young culms. Spikelet with glumes spread out showing two basal male flowers of one stamen each and upper male flower of three stamens. The glume subtending the lowest flower was removed.—68. Culm-tip spikelet not associated with a shoot; × 40. The associated scale on right (partially disconnected) subtends the meristematic shoot rudiment shown in dashed outline in its axil. The other laminas are glumes and compose the spikelet proper. The glume at left subtends a male flower of one stamen (shown in dashed outline). Note prolongation of rachilla and second glume. This glume covers a third glume not shown.—69. Young flower with pistil and two stamens; × 40. (Anther of one of the stamens not shown.) Note absence of bristles.

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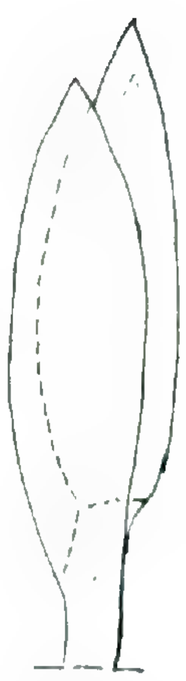

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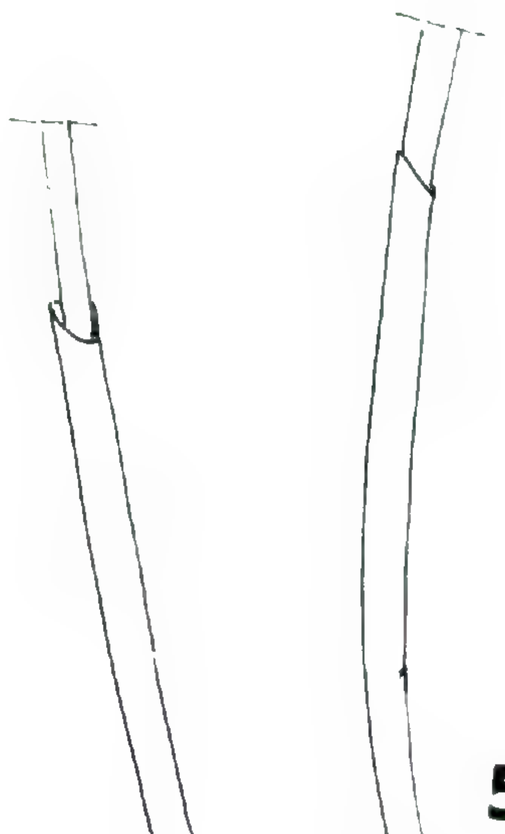

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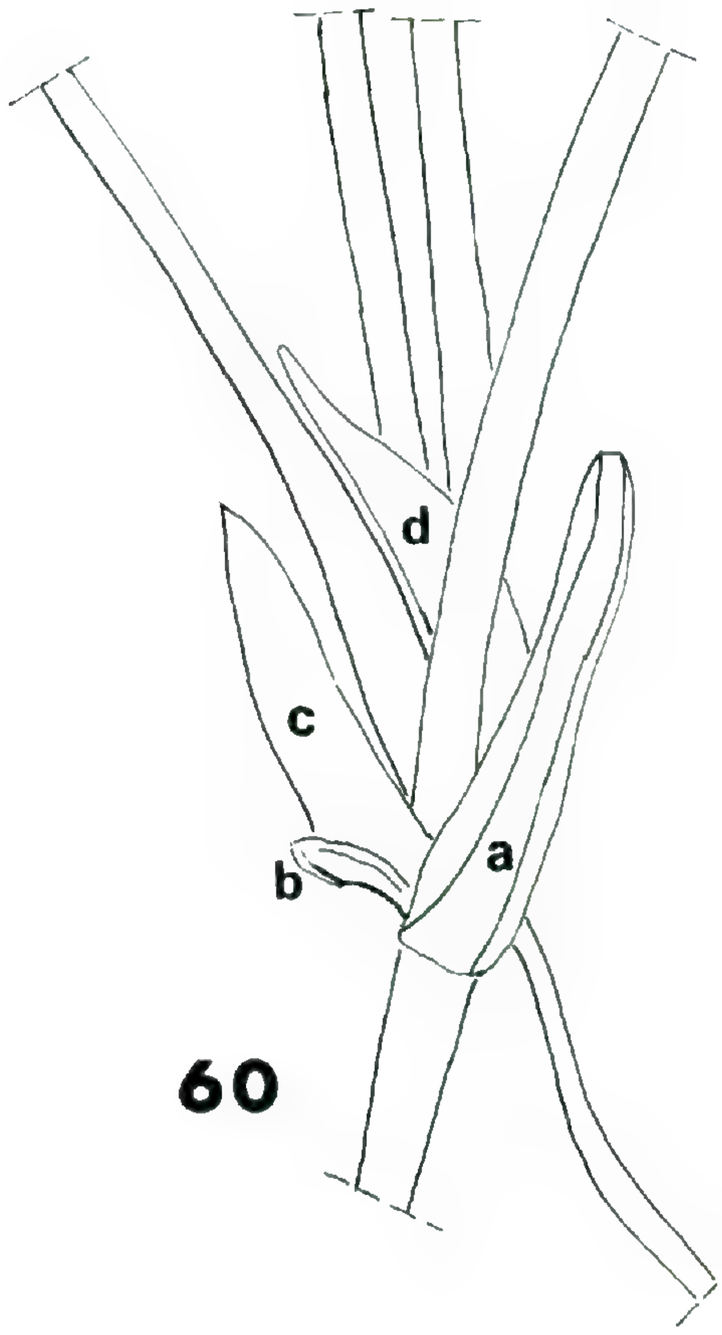

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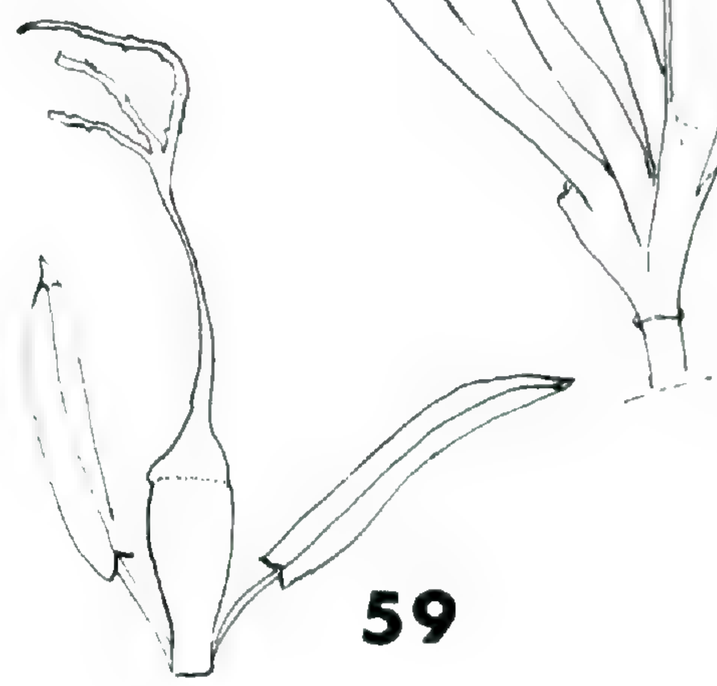

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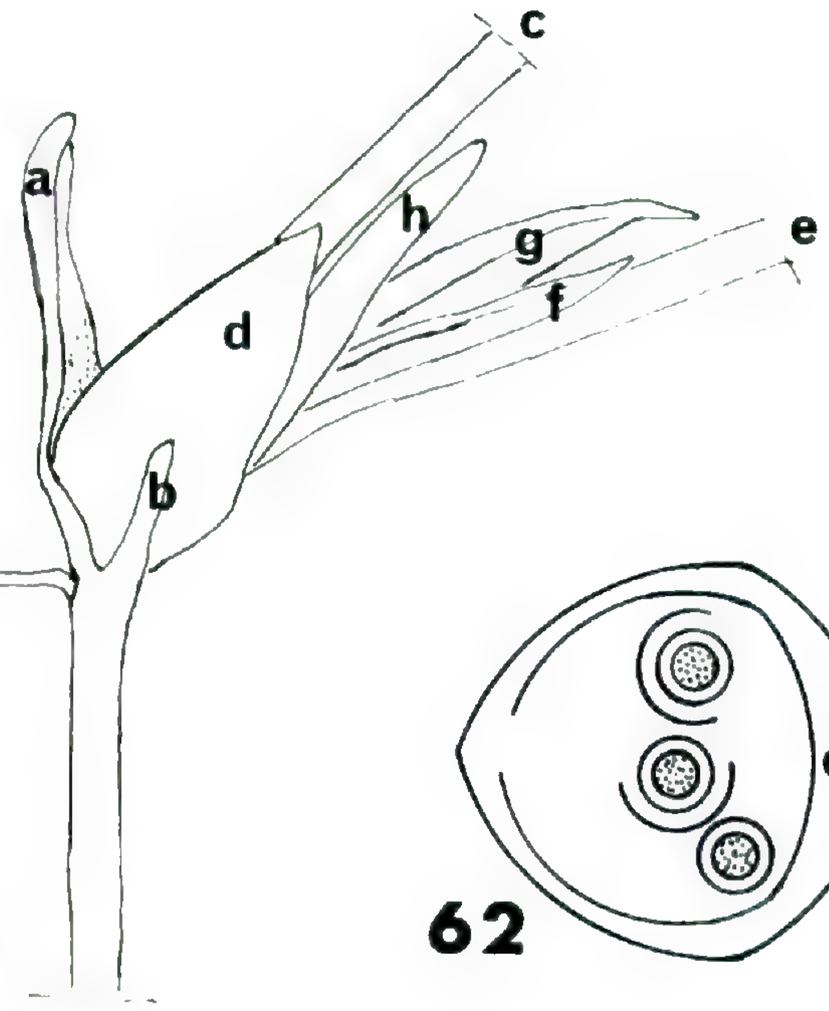

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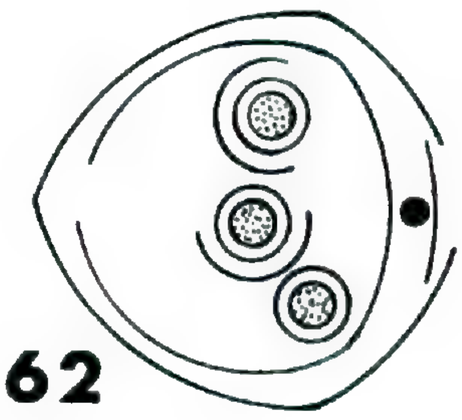

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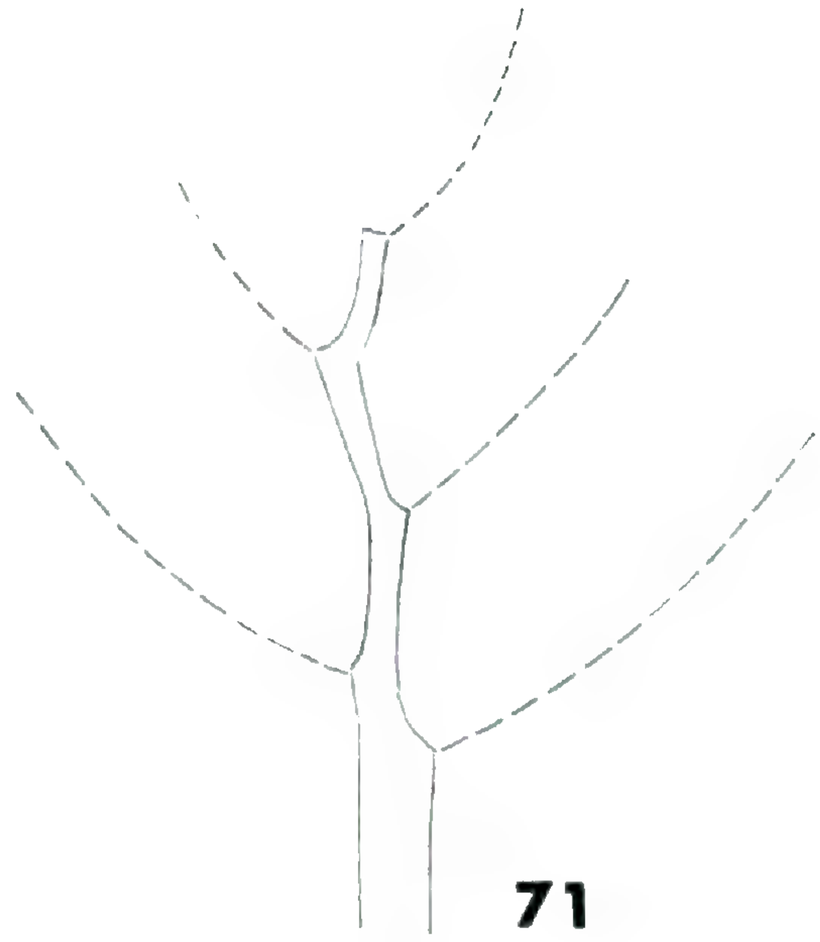


Figures 70–71.—70. Spikelet with four flowers; × 40. The associated scale shown at lower right has had its near side removed to show meristematic shoot rudiment in its axil. On left side is a detached first glume with a female flower in its axil. The three upper glumes have male flowers of 2–3 stamens each.—71. Diagram of spikelet of Fig. 70, showing form of rachilla and (in dashed lines) the position of associated scale and glumes. The interval between flower-bearing glumes usually decreases from base to apex, as here. Compare with Fig. 64, where the basal internode between flowering glumes is not the longest.

from my concept of the spikelet. As a consequence, I consider the rachilla only that part of the axis which starts at the node of the lowest true glume and continues distally. The rachilla bears the other laminar organs to which I prefer to restrict the term "glumes." The dimensions of the spikelets given here, however, include the associated scale when the axillary shoot is in the meristematic stage since this scale is then next to the glumes and difficult to exclude from the measurement; the dimensions given exclude the associated scale and the internode just above it when the shoot is well developed so that this scale is separated from the spikelet proper.

Not counting the associated scale, the spikelet in the type material has 3–5 delicate glumes disposed spirally or they are almost distichous. The associated scale, as stated, always has a meristematic or developed shoot in its axil; the glumes have flowers or are empty. The first true glume frequently has a bisexual or male flower, rarely a female flower, or is empty; sometimes the exact nature of the structure in the axil of this glume cannot be made out. The flowers in the second glume are bisexual or male, or rarely absent. The third glume may be empty, but usually has a male or bisexual flower. The fourth and fifth glumes usually are lacking, or when present are empty or the fourth has a male flower (Fig. 72). The rachilla is slightly zigzag (Figs. 64, 71).

The bisexual flowers have one pistil and 1–3 stamens; the male flowers have 1–2(–3) stamens. The ovary is obovoid-oblong, trigonous, topped by the conic

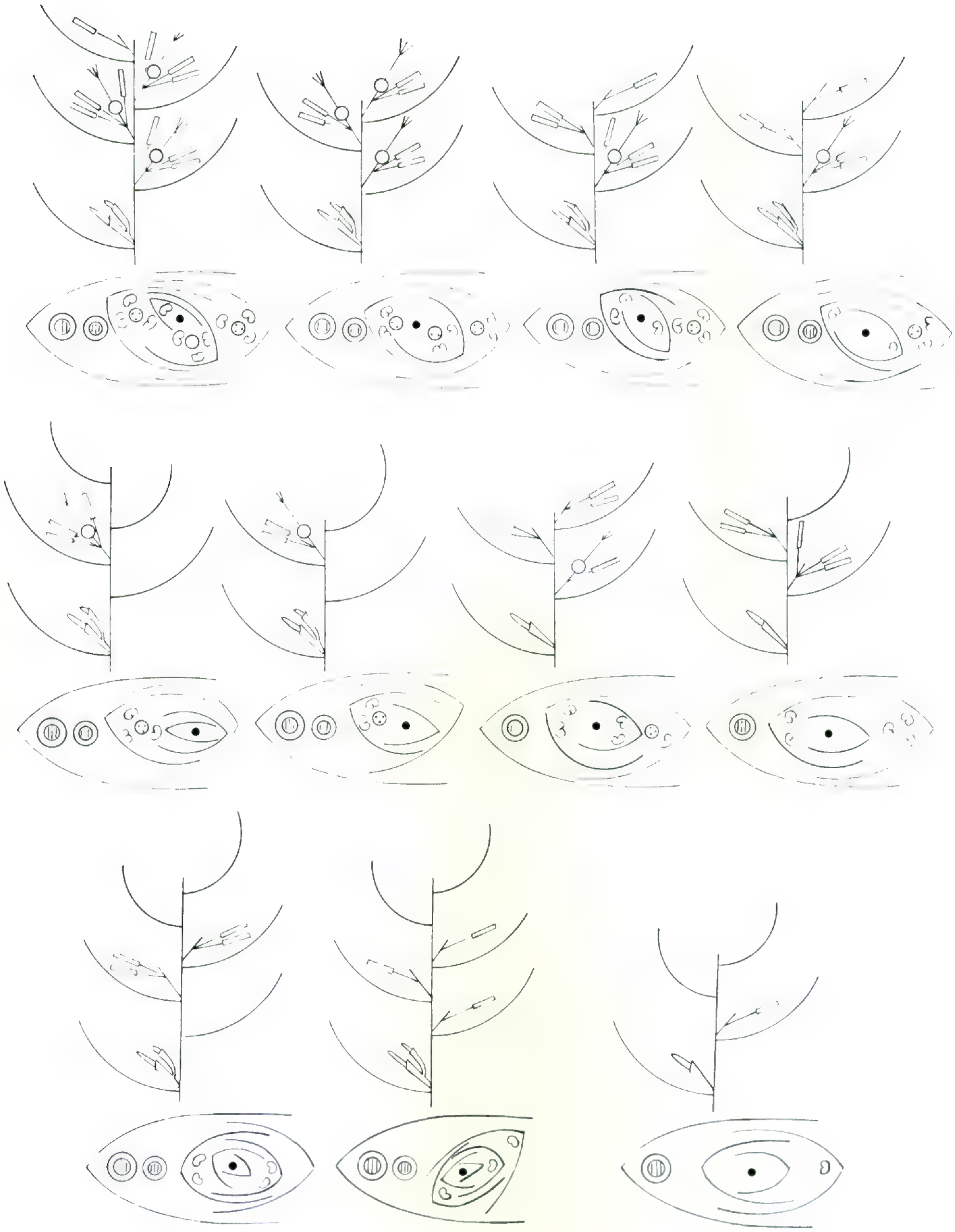
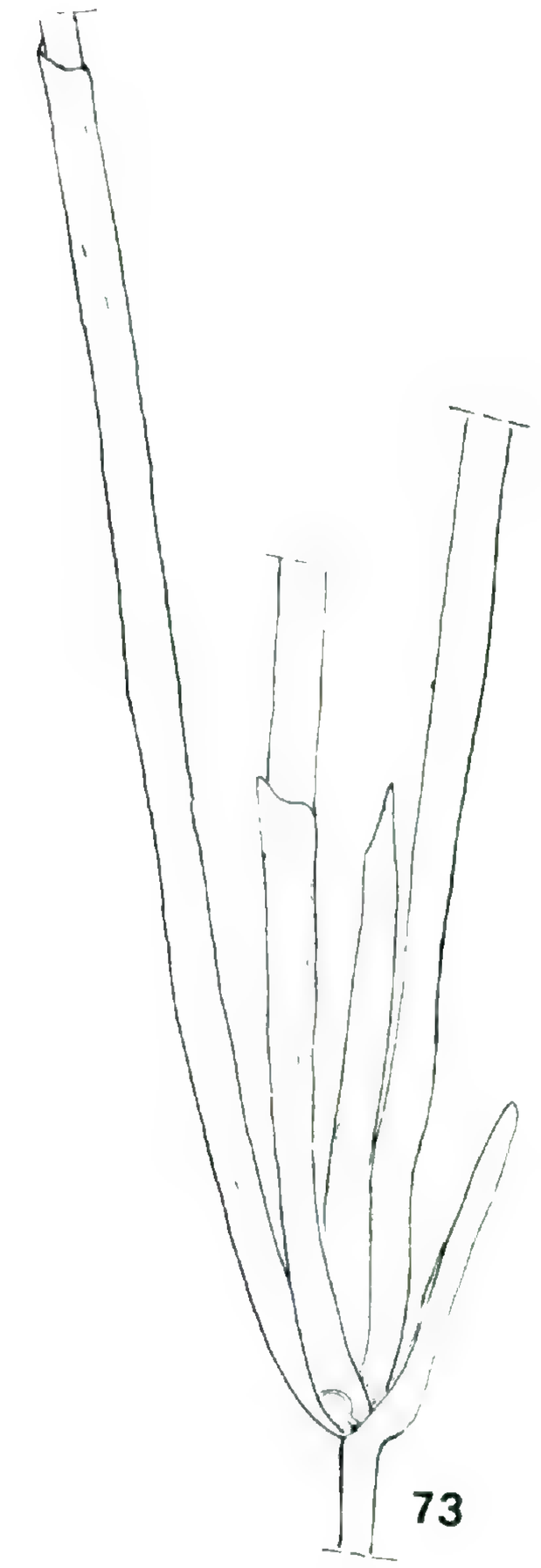


FIGURE 72. Branching patterns and floral diagrams of spikelets found in the syntypes of *Helonema estrellense* Süss.; *Luetzelburg 14027 & 14062*. All the parts shown were actually seen. There is variation in the number of glumes and flowers, in the number of stamens in a flower, and in sex of flowers. In all the spikelets there was a meristematic or developed shoot in the axil of the basal scale, here shown conventionally in the meristematic form. In the floral diagrams, the shaded circles represent culms (surrounded by a single circle representing the upper leaf sheath, the lower sheath not shown); the dark spot represents the apex of the rachilla.



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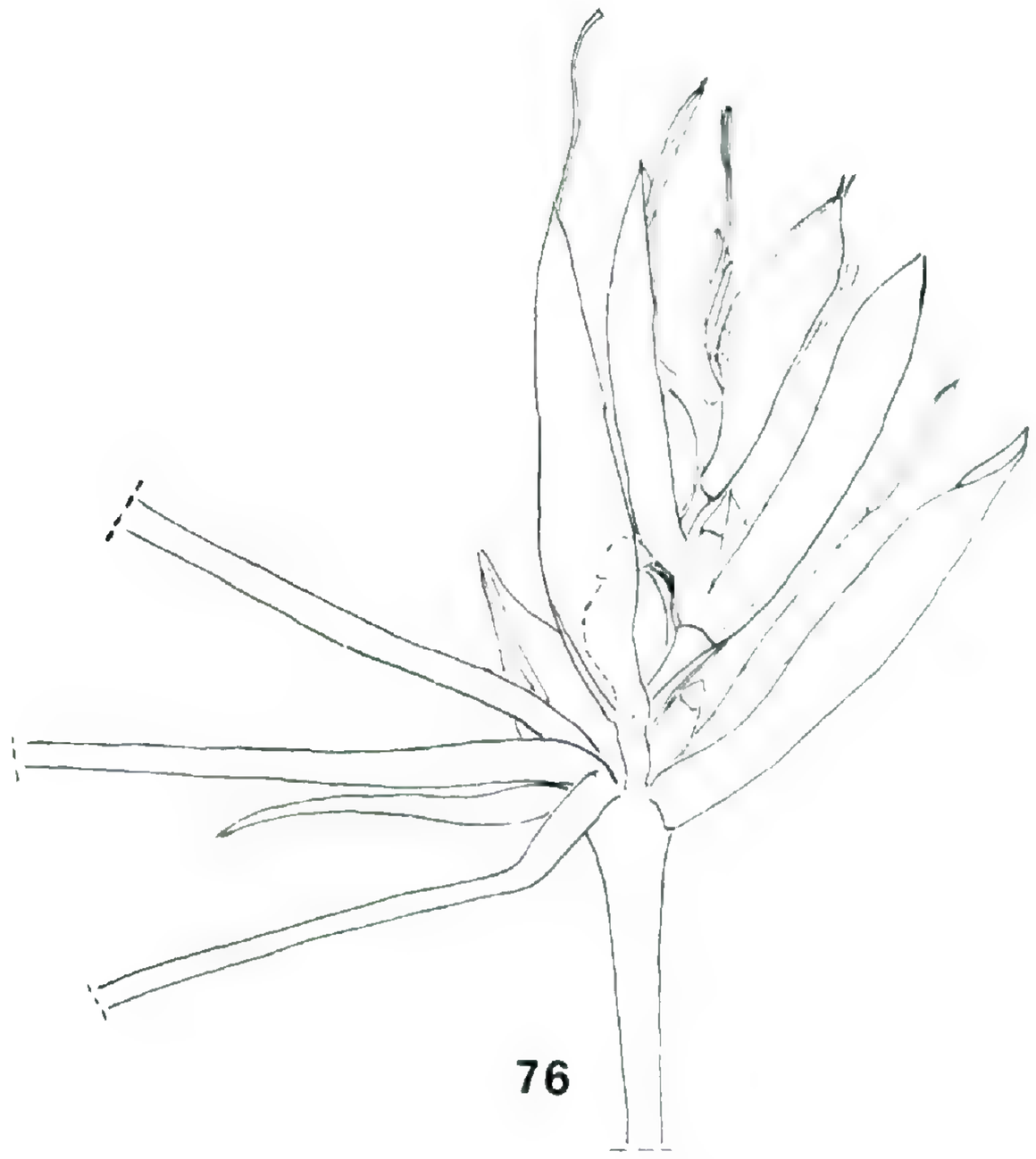

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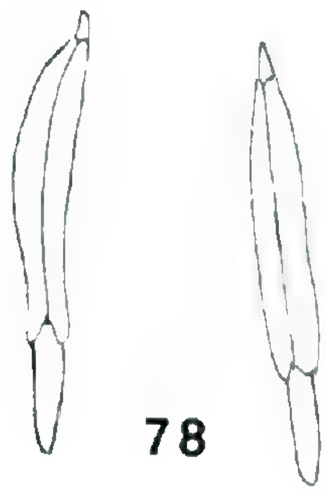

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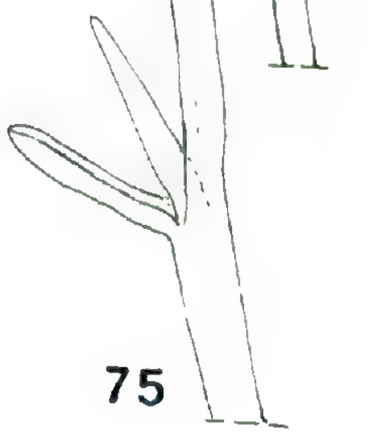

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stylebase which is slightly thickened and of a darker color than the body of the ovary. There are always three stigmatic branches. The anthers are apiculate and the base sagittate (Figs. 59, 69). Mature fruits and bristles were not found in the syntypes.

Süssenguth (1943) based his new genus *Helonema* on two Luetzelburg collections. I examined the sheets of these same collections and the above description was made from them. The spikelets were not much developed and contained male flowers as well as bisexual ones. But from the characters of the plant and its spikelet I early concluded that *Helonema* was really a species of *Eleocharis* (Eiten, 1961).

However, from this material only, the generic relationship could not be absolutely proven, nor whether the species was new or not. It was necessary to collect topotypes and cultivate them to obtain mature spikelets.

Living material was not found in the locality of one of the syntypes, which is a rock-bed stream in the canyon, "Grota do Inferno," cut into the steep seaward face of the Serra dos Órgãos just south of Teresópolis. It was found in the locality of the other syntype, in the small stream, Rio Gongoxoco (as it is now spelled), 2 km east of the railroad station and village of Saracuruna (previously called Rosário), near the main house of Fazenda Anhangá, in the Baixada do Rio de Janeiro, 26 km north of downtown Rio de Janeiro city. The "Baixada" is a flat marshy coastal plain lowland between the seacoast and the foot of the Serra dos Órgãos. The Rio Gongoxoco, therefore, is not in the Serra da Estrela (present spelling) as the label states. This serra starts a few kilometers north, being the steep seaward face of the Serra dos Órgãos leading up from the lowland to Petrópolis. The plant is aquatic and grows submersed rooted in the substrate or pieces float loose on the surface. The plants collected had exactly the same aspect as the type material but were completely sterile when found (Figs. 105–106).

Pieces from a single clone were cultivated submersed in an aquarium for two years and continued to grow in the same branched flaccid filamentous form but did not produce spikelets (Figs. 73–75). However, when ramets of the same

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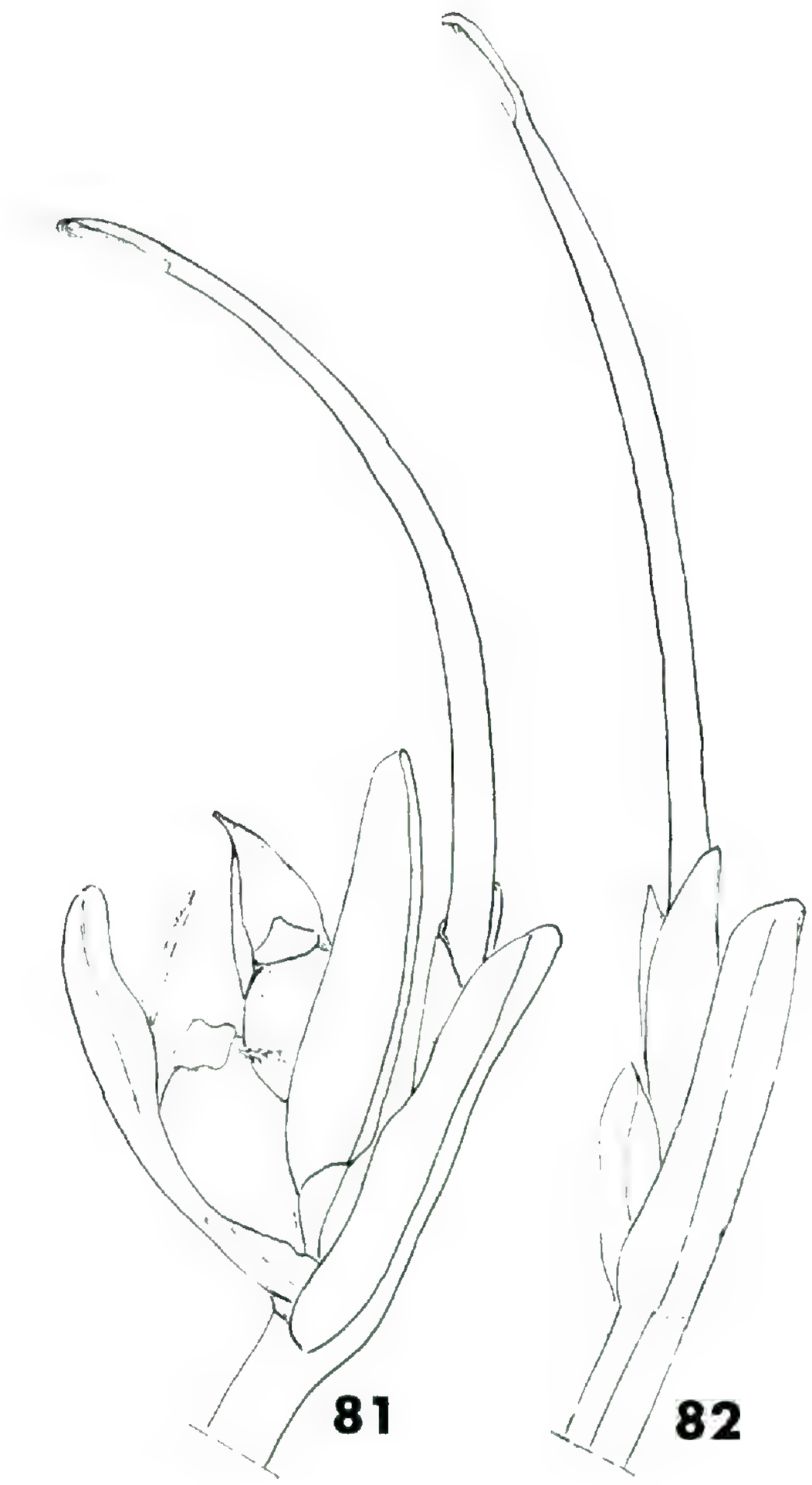
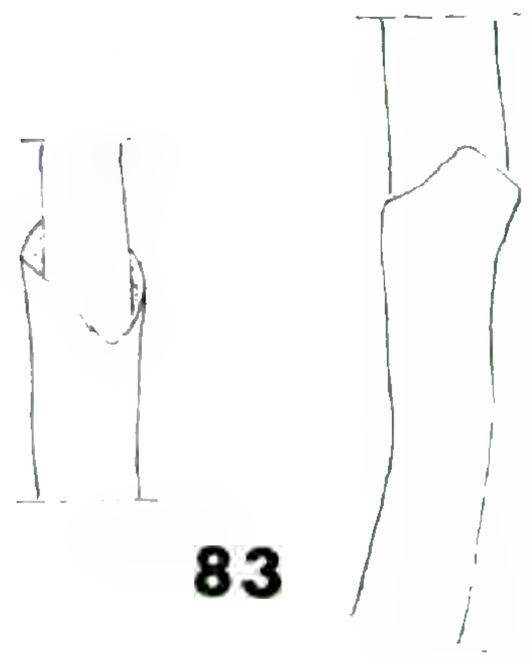
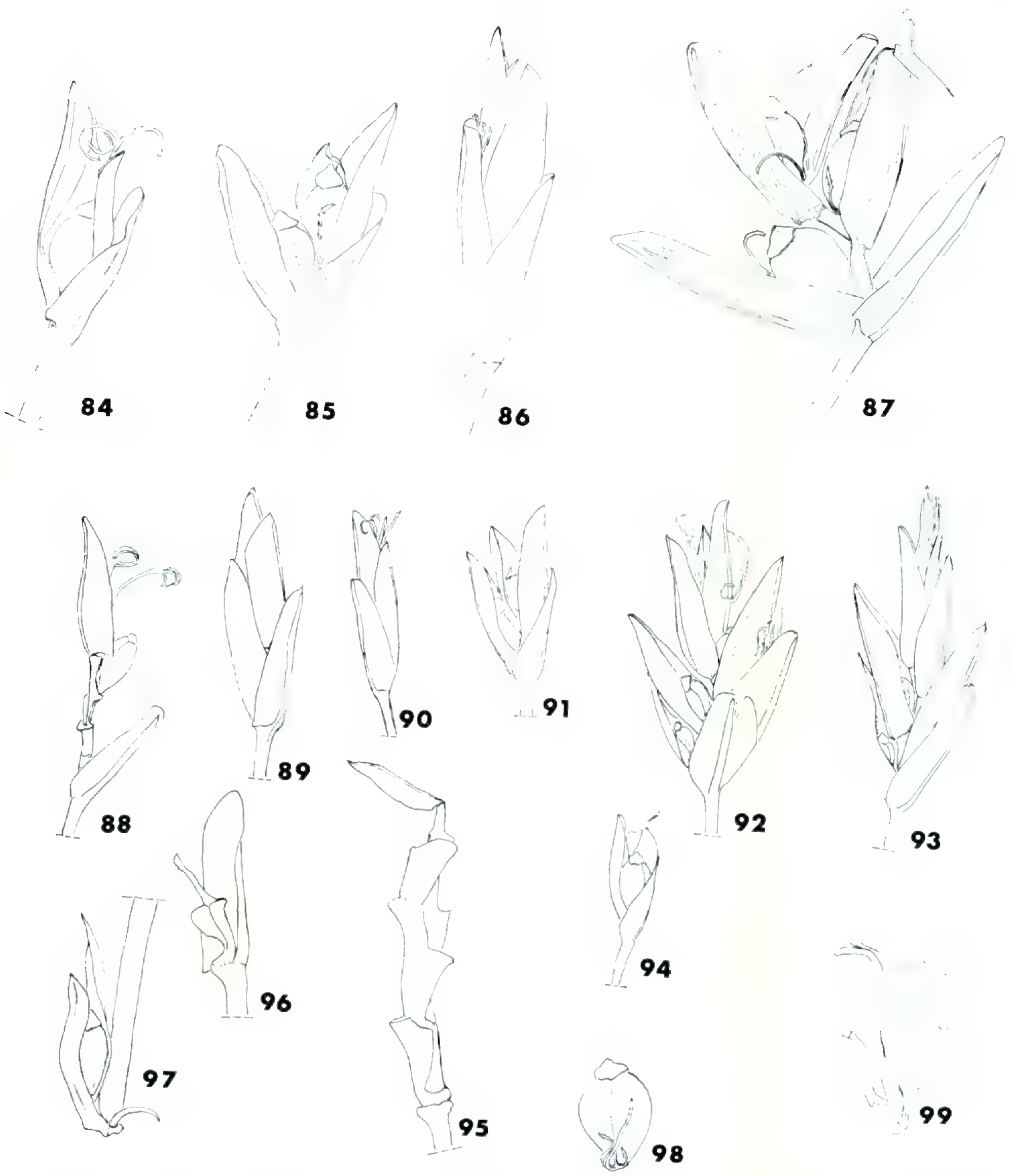
FIGURES 73–80. Topotype of *Helonema estrellense* Süss. (= *Eleocharis minima* Kunth). —73–75. *Eiten & Eiten 7242.* Plant cultivated in an aquarium under constant artificial light. The culm tips were 20 cm below the water surface.—73. Apex of culm with shoot; note lower external bract at base (upper bract and prophylls not seen), three developed culms, and a young culm still within its hood of leaf sheaths; × 16.—74. Tip of culm covered by bracts.—75. Same culm tip with the two bracts spread apart exposing meristematic culm tip; × 27. The plants shown in Figs. 76–108 are of this same clone grown under different conditions.—76–80. *Eiten & Eiten 8054-B.* Same clone as no. *7242*, but cultivated in a shallow, waterproof pot with forest soil covered with a few centimeters of water. The culm tips were 2 cm below the water surface when collected.—76. Culm tip with spikelet and associated shoot. The glumes have been spread apart to show fruits and flowers; × 16. The associated scale is behind the culms.—77. Spikelet without shoot; associated scale and glumes in natural position; × 16.—78. Young stamens with their filaments not yet elongated and anthers not yet shedding pollen; × 45.—79. Mature achene with bristles; × 40.—80. Detail of the square area in Fig. 79 showing the surface pattern of body of fruit; × 160.



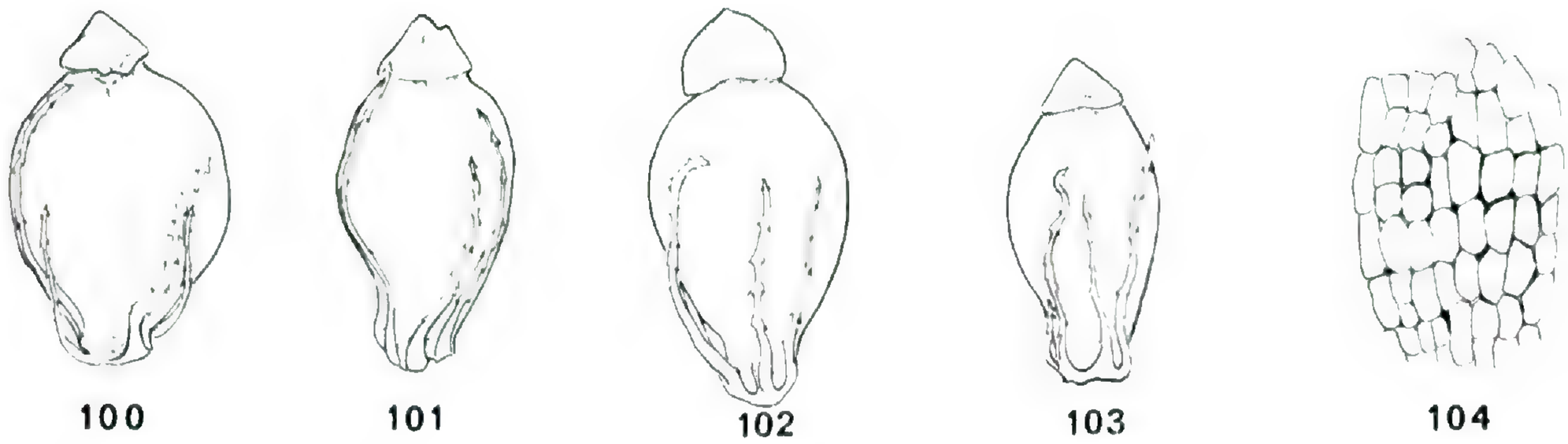


Figures 81–83. *Eiten & Eiten 8054-D*. Same clone as no. *7242* but cultivated in a pot with saturated forest soil, the shoots in air.—81. Culm-tip shoot of one culm with associated spikelet with mature achenes; × 28. Note culm growing from axil of associated scale (equivalent to lower external bract of shoot) and the lower achene in axil of upper bract here acting as lowest fertile glume.—82. Culm-tip shoot of one culm without associated spikelet; × 28. Note the two basal external bracts of the shoot (the lower subtending the new culm) and the two leaf sheaths with oblique mouths.—83. Two views of an inner leaf sheath, showing oblique mouth; × 28.

clone were planted in moist or saturated soil in pots, with the shoots growing in the air, the plants produced a completely different aspect: small tufts of thicker erect culms 2–22 cm tall (Figs. 107–108) with many well developed spikelets. The culms and their leaf sheaths (Fig. 83) were typical of *Eleocharis*, and almost all bore spikelets. Almost always, the spikelets were without associated shoots (Fig. 108: habit; Figs. 77, 86, 89, 90: spikelets in flower; Figs. 84–85, 87–88, 91–97, spikelets in ripe fruit or the fruits already fallen). In some of these cultures a very few of the culms did produce short culm-tip shoots, either without

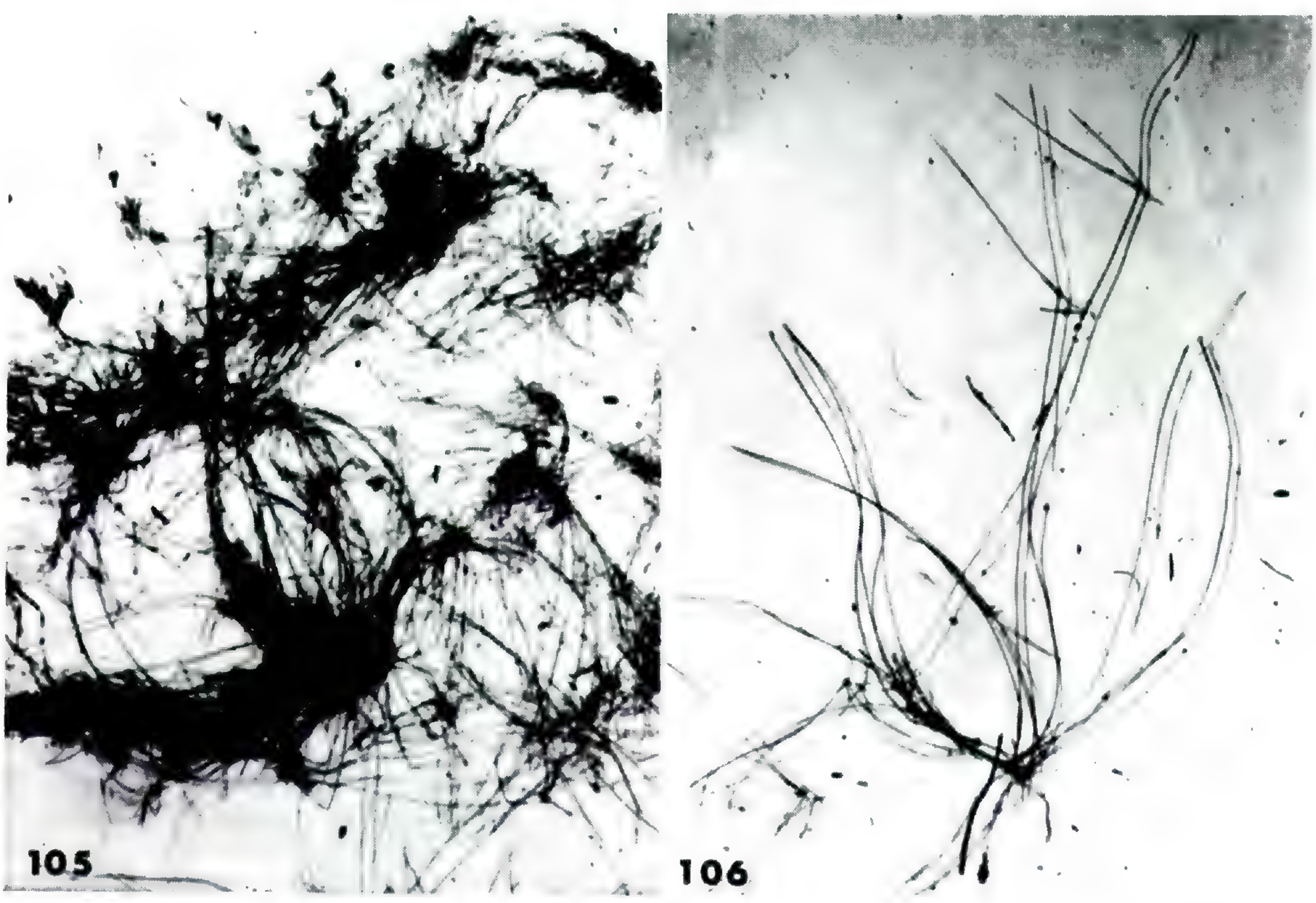


FIGURES 84–99. *Eiten & Eiten 8054-C*. Same clone as no. *7242*, but cultivated in moist drained forest soil in pot.—84–87. Four spikelets (without associated culm-tip shoots) showing variation in number of glumes and fruits; × 19. In Figs. 84–86 the associated scale and glumes are in a natural position; in Fig. 87 they were spread apart. In the plants cultivated in this manner, the associated scale, besides bearing no flower, also does not have a meristematic rudimentary shoot in its axil.—88. Culm-tip spikelet; associated scale and uppermost glume remain, the other glumes have fallen; × 11.5.—89–90. Culm-tip spikelets in flower; × 11.5.—91–93. Culm-tip spikelets in fruit; × 11.5. The spreading apart of the glumes here is natural, caused by the growth of the achenes.—94. Culm-tip spikelet with associated scale and one glume. The single achene from the single lateral flower appears terminal on the rachilla apex; × 11.5.—95. Rachilla of a culm-tip spikelet from which the fruits, associated scale, and all glumes except the empty terminal one have fallen; × 19.—96. Rachilla of a culm-tip spikelet with associated scale still present and its achene and two glumes fallen; × 11.5.—97. Sessile spikelet on a very short axis, arising at base of clump among culm bases; × 11.5. Sessile spikelets are common in plants of this clone in this type of cultivation. Compare with *Eleocharis chamaegyne*.—98. Mature achene from culm-tip spikelet; × 19. Note bristles.—99. Young flower from culm-tip spikelet; × 19. In this stage bristles were not yet formed; they develop during the maturation of the fruits. Detail of stigmatic papillae on upper right.



Figures 100–104. *Eiten & Eiten 8054-C.* Mature achenes from same clone as no. *7242* but cultivated in moist drained soil in pot.—100–103. Achenes from different spikelets showing variation in form of body and stylebase; × 37. Note bristles.—104. Shallow-reticulate surface pattern of a mature fruit; × 93.5.

associated spikelets (Fig. 82) or with associated spikelets (Figs. 81, 107). All the flowers in the spikelets were bisexual with a pistil with three stigmatic branches and 2–3 stamens (Figs. 78, 99). Abundant mature achenes formed, always with bristles (Figs. 76, 79, 80–81, 84–85, 87–88, 91–94, 97–98, 100–104), but these bristles were not present in the young flower stage (Fig. 99). Meristematic vestiges of culm-tip shoots were absent in the axils of the associated scales (empty "lowest glume").



Figures 105–106. *Eiten & Eiten* 7833.—105. Recently collected plant that had grown submersed in its natural habitat in the Rio Gongoxoco photographed in a tray with water; × 0.5. (Collected in wild from same clump as no. *7242*.)—106. Single shoot; × 0.5. The plant floating in water in tray and its shadow make a double line.

Apparently, then, when the plant grows completely under water so that the culm tips are at least several centimeters under the surface, spikelets do not form, only well developed culm-tip shoots. When the plant is under water but the culm tips are near or at the surface (as in the case of the syntypes), small flowering spikelets (which probably do not go to seed) form on a few of the culm tips and developed or at least meristematic culm-tip shoots always form in the axil of the associated scale. When the plant or at least its culm tips is completely in the air, well developed, seed-bearing spikelets form which do not bear culm-tip shoots in the axil of the associated scale, not even in the meristematic form, or only bear such shoots extremely rarely. Water around the culm tip thus seems to discourage spikelet and seed formation and encourage vegetative shoot formation.

The habit and achenes of the topotype grown in and out of water prove that *Helonema* is really only an extreme submerged-aquatic ecological modification of a species of *Eleocharis*, *E. minima* Kunth. The plant fits perfectly the description of the species in Svenson's (1937) monograph.

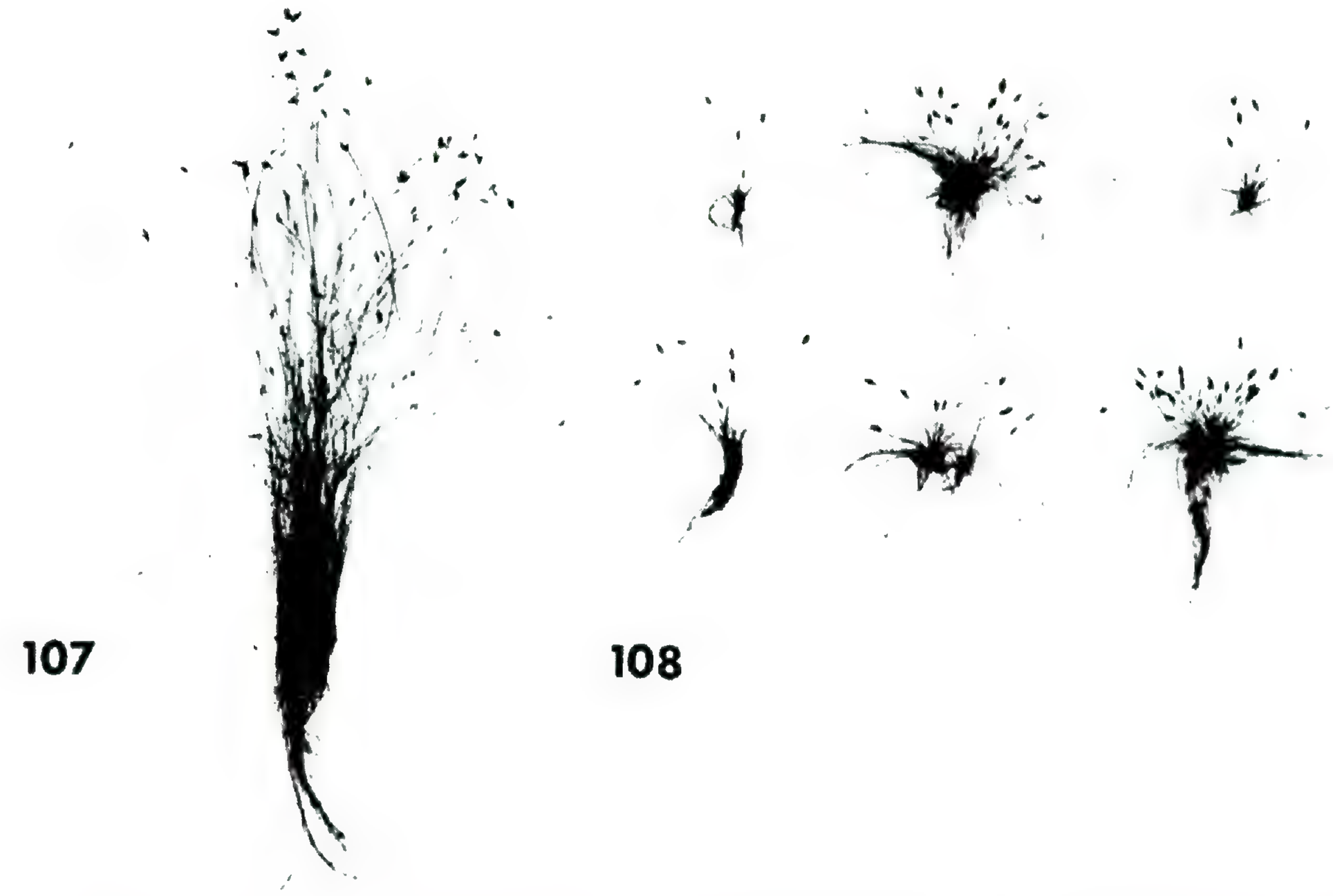
Svenson (1937) states that in Brazil, *Eleocharis minima* has an aquatic phase, known as var. *ambigua* (Steud.) Kük. The drawing he gives for this variety (his Plate 462, Fig. 4) shows a tufted plant with erect stems with spikelets; from the base of two of the spikelets a few roots grow out. This habit is almost identical to the typical terrestrial habit of the species; it is definitely not the habit of *Helonema*. Since ramets of the same clone develop the *Helonema* habit when grown submersed and the typical *E. minima* habit when grown emersed, the *Helonema* habit is not a genetic form and should not have a formal taxonomic name. Since the variety *ambigua* is even less different from the typical form and is also very unlikely to be a genetically fixed form, it should not be maintained as a variety.

Other collections of *Eleocharis minima* studied (det. L. T. Eiten):

Eleocharis minima Kunth var. *minima* (topotypes of *Helonema estrellense* Süss., all in herb SP. Duplicates of the following collections will be distributed to other herbaria.)

BRAZIL. RIO DE JANEIRO: Mun. de Duque de Caxias, Fazenda Anhangá, 22°40′S. 43°14′W., Rio Gongoxoco, 100–200 m from its mouth in the Rio Imbariê, plant submersed in clear water near bank, 25 Apr. 1966, *Eiten & Eiten 7225, 7228, 7233, 7234, 7235*. Same place, plant rooted in substrate, submersed in 0.5 m of clear water, 25 Apr. 1966, *Eiten & Eiten 7226*. Same place, mouth of Rio Gongoxoco where it empties into Rio Imbariê, plant growing fixed to concrete wall of small dam, submersed under 2 dm of clear water, 25 Apr. 1966, *Eiten & Eiten 7240*. Same place, plant growing as large cushion over drainage pipe, submersed in 3 dm of clear water, 25 Apr. 1966, *Eiten & Eiten 7241, 7242, 7243*. Same place, plant growing as a cushion over drainage pipe, submersed in 6 dm of clear water (from same clump as no. 7242), 20 Nov. 1966, *Eiten & Eiten 7833*. Mun. de Itaguá, Instituto de Pesquisa e Experimentação Agrícola do Centro-Sul, topotype material of *Eiten 7242* cultivated in continually saturated soil, 19 Nov. 1966, *Eiten & Eiten 7800*. Same place, same topotype material, cultivated in continually saturated soil, 21 Nov. 1966, *Eiten & Eiten 7878*. SÃO PAULO: Mun. de São Paulo, city of São Paulo, Parque do Estado, Instituto de Botânica, same topotype material (*Eiten 7242*) cultivated submersed in 25 cm of water, tips of culms floating on surface, Mar.–Apr. 1967, *Eiten & Eiten 8054-B*. Same place, same topotype material, cultivated emersed in pot, rooted in moist drained soil, Jan.–Feb. 1967, *Eiten & Eiten 8054-C*. Same place, same topotype material, cultivated emersed in pot, rooted in saturated soil, Mar.–Apr. 1967, *Eiten & Eiten 8054-D*.

Eleocharis minima Kunth var. *minima* (aquatic habit like that of *Helonema*).



FIGURES 107–108. Cultivated topotypes.—107. *Eiten & Eiten 7878*. Same clone as no. *7242* but cultivated emersed in continually saturated soil in the Baixada do Rio de Janeiro; × 0.3.—108. *Eiten & Eiten 8054-D*. Same clone as no. *7242* but cultivated emersed in continually saturated soil in São Paulo city; × 0.5.

UNITED STATES. FLORIDA: Seminole Co., Lake Adelaide, on bottom and floating, 10 Sep. 1955, *Schallert 24132* (UB).

BRAZIL. PARÁ: Rio Itacaiuna, Seco-Grande, 20 June 1949, *Fróes & Black 24608* (UB).

Eleocharis minima Kunth var. *minima* (terrestrial habit).

BRAZIL. PARÁ: Almeirim, campo inundado do Jutahy, flutua na água, 14 Apr. 1923, *Ducke s.n.* (RB). MARANHÃO: perto de Carolina, [wet place in region of] campo cerrado, 26 May 1950, *Pires & Black 2179* (IAN). MATO GROSSO: Corumbá, parte alagável da margem do [Rio] Paraguay, 20 Oct. 1953, *Pereira et al. 164* (RB). BAHIA: *Bondar 37162* (SP). This collection has basal spikelets with mature fruits. RIO DE JANEIRO: Petrópolis, Caetitu, brejo, Mar. 1944, *Góes & Constantino 289* (RB). SÃO PAULO: Mun. de São Paulo, city of São Paulo, Barra Funda, July 1885, *Loefgren 9186* (SP). Mun. de Mogi-Mirim, aquática submersa, 25 May 1927, *Hoehne 20513* (SP). Mun. de Mogi-Guaçu, Fazenda Campininha, brookside, saturated

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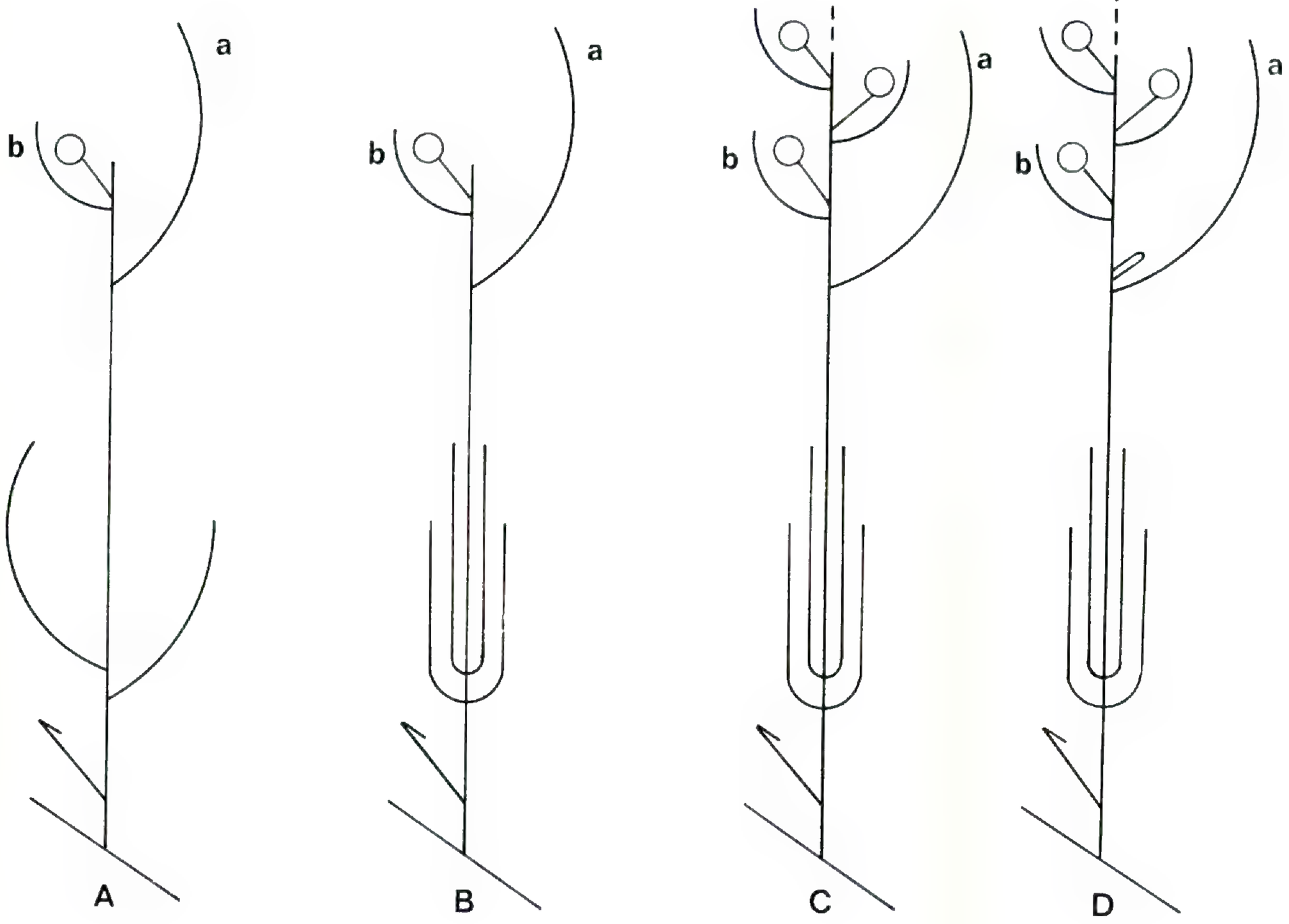
FIGURE 109. Structure of culm and its appendages in *Eleocharis* and its derived genera, *Websteria* and *Egleria*.—A. Short axis of *E. chamaegyne*.—B. Long axis (culm) of *E. chamaegyne* and other *Eleocharis* spp. with 1-flowered spikelets and of *Websteria*.—C. *Eleocharis* spp. with many-flowered spikelets and *Egleria*.—D. Culm with spikelet and vestigial vegetative shoot in axil of associated scale in syntypes of *Helonema* (*E. minima*).—E. *Eleocharis* spp. with spikelet and associated culm-tip shoot.—F. *Eleocharis* spp. and *Websteria* with culm-tip shoot without associated spikelet.—G. *Eleocharis* spp. with vestigial spikelet (such as *E. interstincta*).—H. *Eleocharis* spp. culm whose tip bears neither shoot nor spikelet. Note homology of associated scale, a, to lower external bract at base of a culm-tip shoot, d, and to lower bract of a culm tip without shoot or spikelet, f; and homology of lowest true glume of a spikelet, b, to upper external bract at the base of a culm-tip shoot, e, and to upper bract of a culm tip without shoot or spikelet, g.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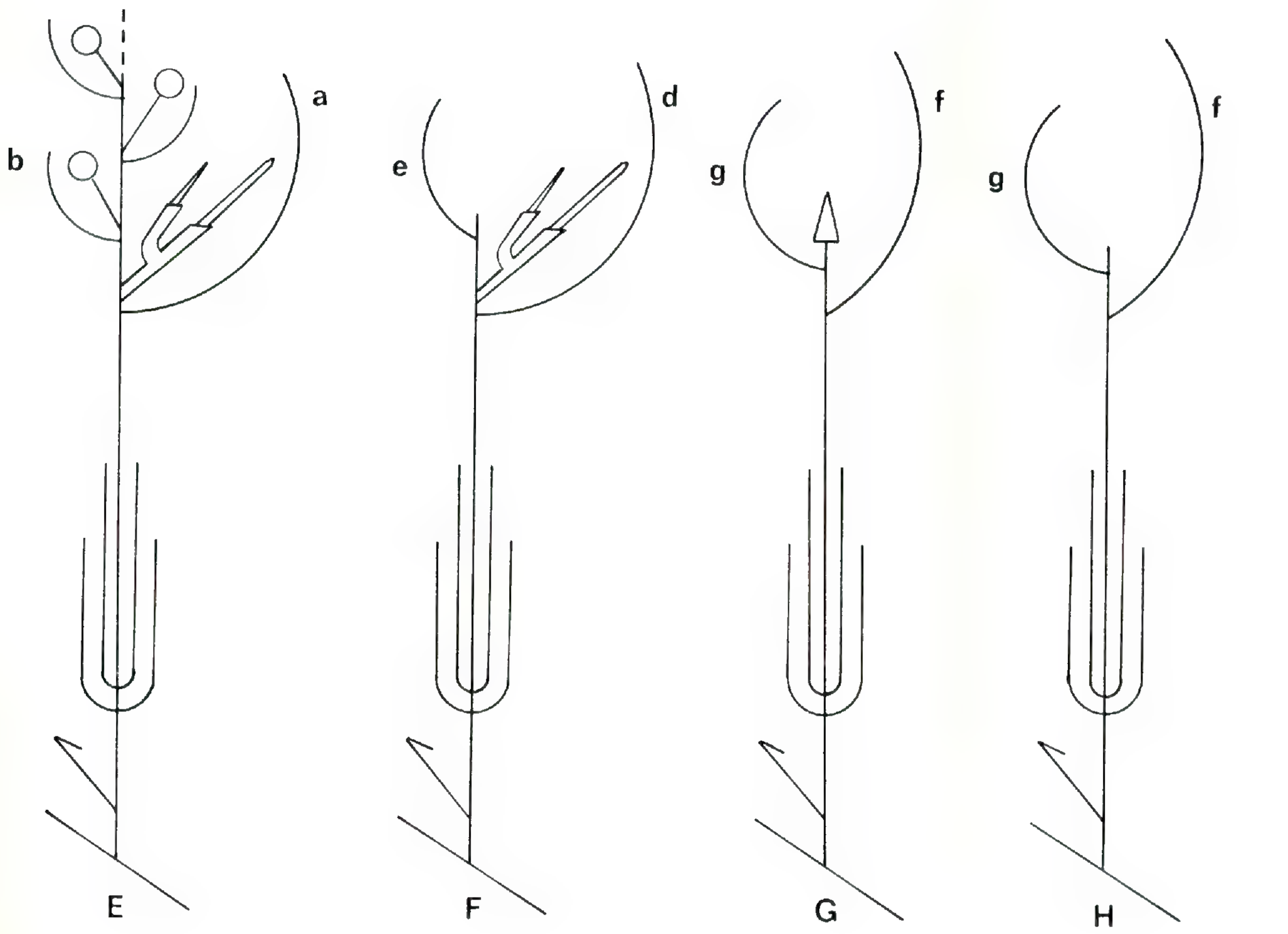
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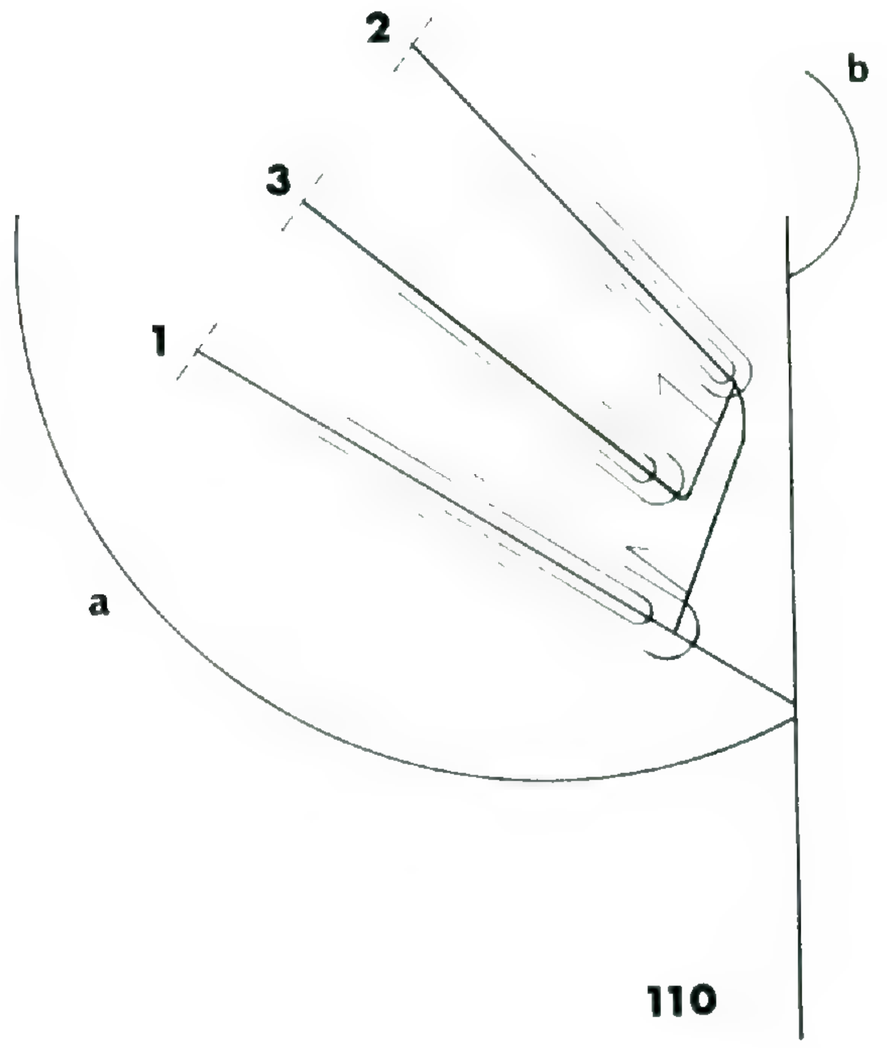

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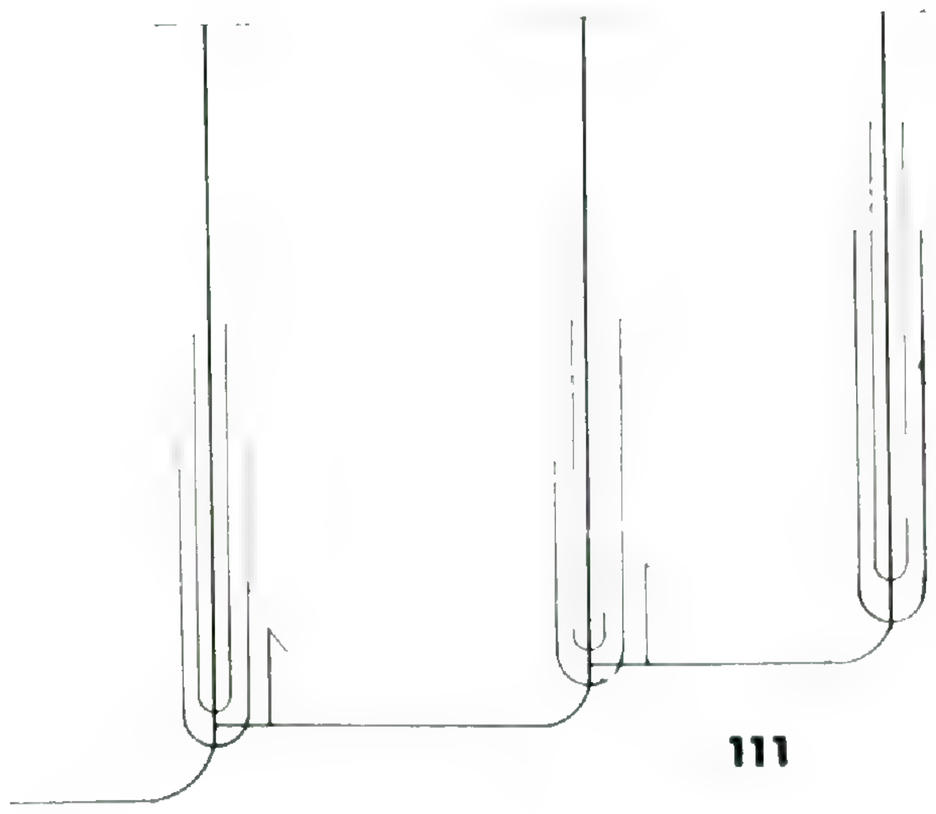

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FIGURES 110–111.—110. Branching pattern and relation of leaf sheaths and prophylls in a culm-tip shoot of *Eleocharis* and *Websteria*. Three culms (numbered in the order of their appearance) are shown in this shoot. Note that the first culm, although a branch, does not bear a prophyll but the other culms do. The new culms are shown here arising in the axil of the lower leaf sheath but in some species they appear to arise in the axil of the upper leaf sheath. Note that the prophyll on the axis of culm 2 (addorsed to culm 1) has become separated from the leaf sheaths of its culm by the growth of culm 3. a = lower external bract at base of shoot; b = upper external bract at base of shoot.—111. Branching pattern of rhizome and culms in *Eleocharis*. The prophyll of a culm axis is at some distance from the leaf sheaths of that axis when the rhizome internodes are long. Note that the rhizome is sympodial, made up of the first two basal internodes of each succeeding branch. The first of these two basal internodes is the short subprophyllar internode (between the origin of the axis and the prophyll node); the second is the longer internode between the prophyll node and the node of the lower leaf sheath on the upturned part of the axis that forms the culm. When older, more culms may arise at a rhizome node, the branching being the same as that shown in Fig. 110. The bases of all the culms at one rhizome node then thicken and become concrescent, forming a corm, which is the solid center of a tuft of culms.

soil, 22 Apr. 1960, *Eiten & Eiten 1986* (SP, UB). Same place and habitat, 23 Sep. 1960, *Eiten & Eiten 2397-A* (SP).

PARAGUAY: Near Puerto Casado, 22 Oct. 1893, *Lindman 2295* (R). Cited in Svenson's monograph (1937).

Eleocharis minima Kunth var. *bicolor* (Chapman) Svenson (terrestrial habit).

BRAZIL. SÃO PAULO: Mun. de Mogi-Guaçu, Fazenda Campininha, brookside, saturated soil, 3 Sep. 1960, *Eiten & Eiten 2301-A* (SP).

Figure 109 gives diagrams of the structure of culms and spikelets in *Eleocharis* and the related genera *Websteria* and *Egleria* (Eiten, 1964) to illustrate the terminology used in this paper. The figure shows several homologies: (1) between the lower, usually two short scales on the short axis of *E. chamaegyne* and the usual two leaf sheaths in the genus; (2) between the associated scale at the base of the spikelet and the lower of the two external bracts at the base of a culm-tip shoot, and between them and the lower of the two scalelike bracts that covers a culm tip without shoot or spikelet; (3) between the lowest true glume of a spikelet (that which bears the lowest flower) and the upper external bract at the base of a culm-tip shoot, and between them and the upper scalelike bract

of a culm tip without shoot or spikelet. The prophyll is shown in Fig. 109 next to the leaf sheaths of its own axis, but when the next culm of the shoot develops, this will often grow between this prophyll and the leaf sheaths, thus separating them. The third culm to develop (from the base of the second culm) will separate the first prophyll and the leaf sheaths of its axis even more, etc. (Fig. 110). Only the first culm in a culm-tip shoot does not bear a prophyll. A prophyll will also be separated from the leaf sheaths of its axis when the culm is the upturned end of an axis whose lower two internodes form part of a rhizome (Fig. 111).

Figure 109 shows that the lamina called the associated scale never bears a flower and for this reason I prefer not to call it a glume. It may be empty or bear a vestigial or developed culm in its axil, which in turn may bear a culm at its base in the axil of a leaf sheath, and this another culm, etc., so forming a shoot (Fig. 110). This is not a case of vivipary in the strict sense for the shoot does not arise from a seed germinating while still on the plant; neither is it a case of vivipary in a looser sense, for the shoot never grows from the axil of a true flower-bearing glume. It grows out only from this one location, which never does bear a flower. The associated scale in *Eleocharis* and its derived genera seems to be of a different nature from the empty, non-prophyll, lower glumes in other genera such as *Rhynchospora*, *Cladium*, etc., which never bear vegetative shoots in their axils and which can be considered to be flower-bearing true glumes that have become sterile.

Bisboeckelera paporiensis Süss.

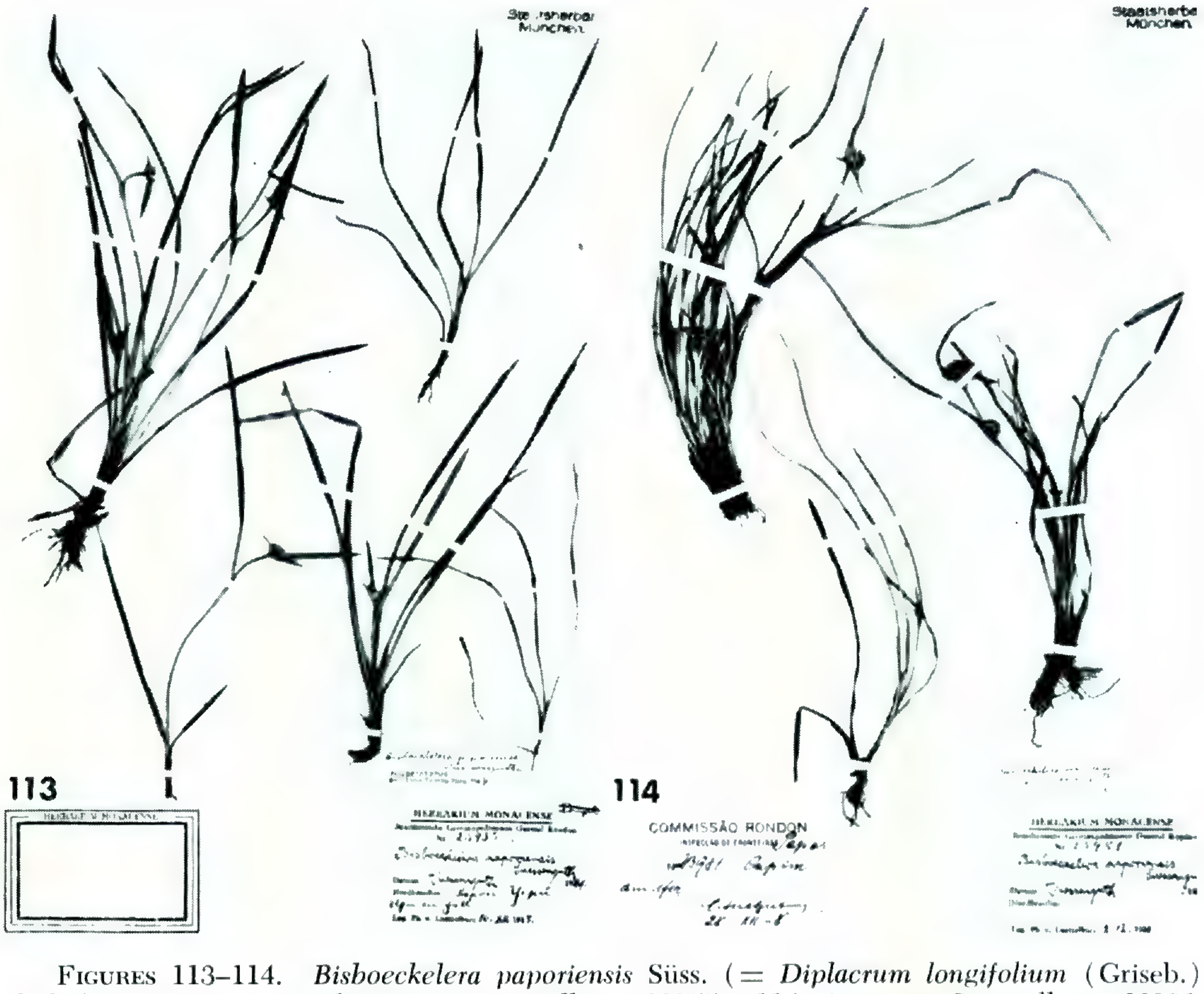
(= *Diplacrum longifolium* (Griseb.) Clarke)

Description of syntypes of *Bisboeckelera paporiensis* Süss., Bot. Jahrb. Syst. 73: 120–121. 1943: Grenze Brasilien-Kolumbien, Gebiet des Rio Papori, Yapú, Ufer am Fall, 16 Dec. 1928, *Luetzelburg* 23955 (M). Ebenda Capim am Ufer, 8 Dec. 1928, *Luetzelburg* 23981 (M).

The plant is 20–35 cm tall with culms 5–20 cm long, triangular in cross section with concave faces and salient veins (Figs. 112–115). Each culm has 2–3 basal leaves 15–22 cm long and 2.7–3.5 mm wide; the leaves are flat, linear, with visible small teeth on the margins near the apex, and have 15 veins, of which two lateral ones are evident and denticulate near the apex. The sheath is 2.0–3.0 cm long, purplish-red, the contralaminar side (the side opposite to the side which bears the blade) membranous and the mouth with a triangular appendage 1.5 mm long.

The inflorescence is made up of 1–2 heads (capitula) 5–12 mm wide and 5–7 mm tall; when there are two heads in an inflorescence the lower is always smaller. There is one cauline leaf 8.5–19.5 cm long and 2.5–3.5 mm wide. On culms with two heads, this leaf subtends the lower head (Fig. 115). Three visible bracts are associated with the upper head; these in order have the following lengths: 2–6 cm, 1–3.5 cm, and 0.8–1.7 cm. The other bracts, inside the heads, are very small and not evident. The peduncles of the heads are 0.8–8.5 cm long.

FIGURE 112. Lectotype sheet of *Bisboeckelera paporiensis* Süss. (= *Diplacrum longifolium* (Griseb.) Clarke); *Luetzelburg* 23955; × 0.4. Figures 116–118, 131–153 were made from plants of this collection.



FIGURES 113–114. *Bisboeckelera paporiensis* Süss. (= *Diplacrum longifolium* (Griseb.) Clarke); × 0.2.—113. Isolectotype; *Luetzelburg 23955*.—114. Syntype; *Luetzelburg 23981*. Figures 119–130 were made from plants of this collection.

Each head is made up of structures having a variable branching pattern and containing the flowers. These groups are here called "fascicles." Details of their branching and concepts of the "spikelet" are discussed below.

The male flower consists always of only one stamen. The female flower is a single pistil with a trigonous straw-colored ovary and a rusty-brown style with three stigmatic branches (Fig. 116).

The apparently mature fruit is ellipsoidal to obovoid, 1.3–1.5 mm tall and 0.9–1.0 mm wide, with a dark brown apiculate apex and a bright straw-colored body with vertical grooves and three vertical ridges. The fruit has a shallow light green cupule at the base with three projections corresponding to the three ridges (Figs. 117–118).

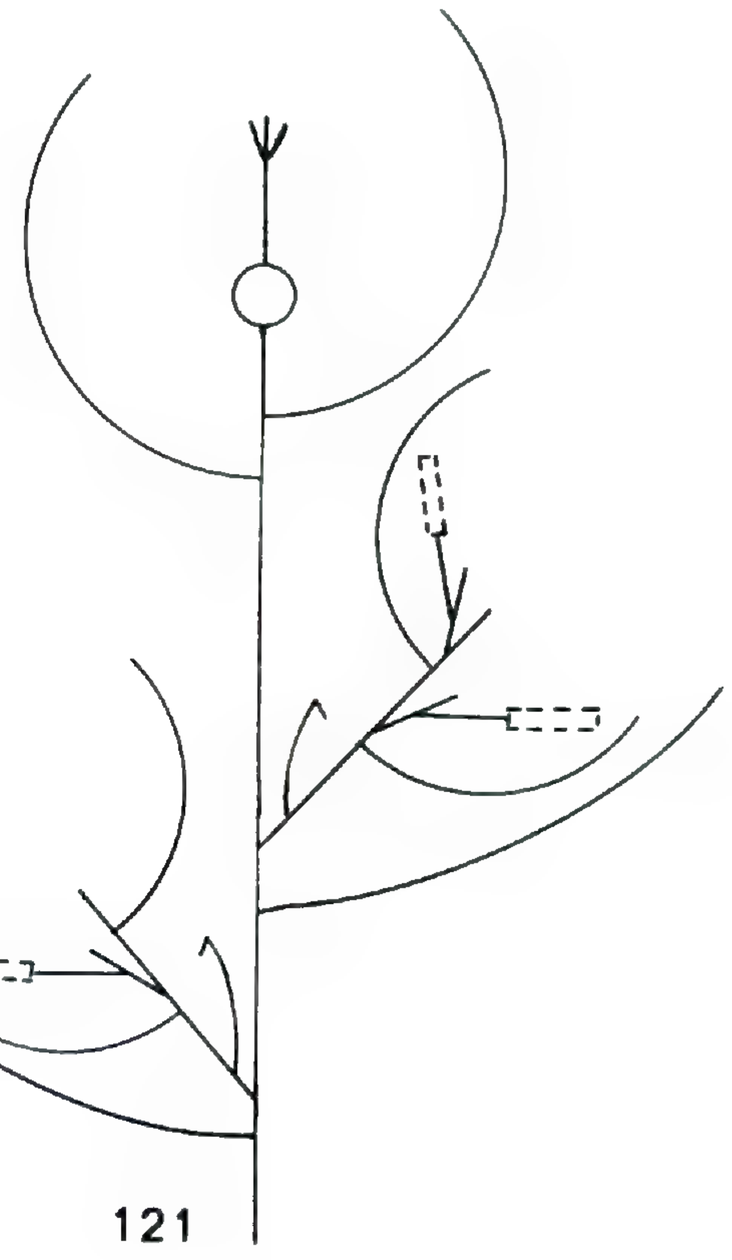
As mentioned, the inflorescence is made up of 1–2 heads in the syntype collections. Each head is made up of fascicles which are more or less distinct bodies containing the last few branch orders. The fascicles are smaller and less distinct the more distally they arise in the head. In the basal fascicles of a head, one can distinguish without difficulty the subtending bract of the fascicle, its few-millimeters-long peduncle, and its prophyll. The apical fascicles are small and very crowded together; it is difficult to analyze them and find their subtending bracts and prophylls.

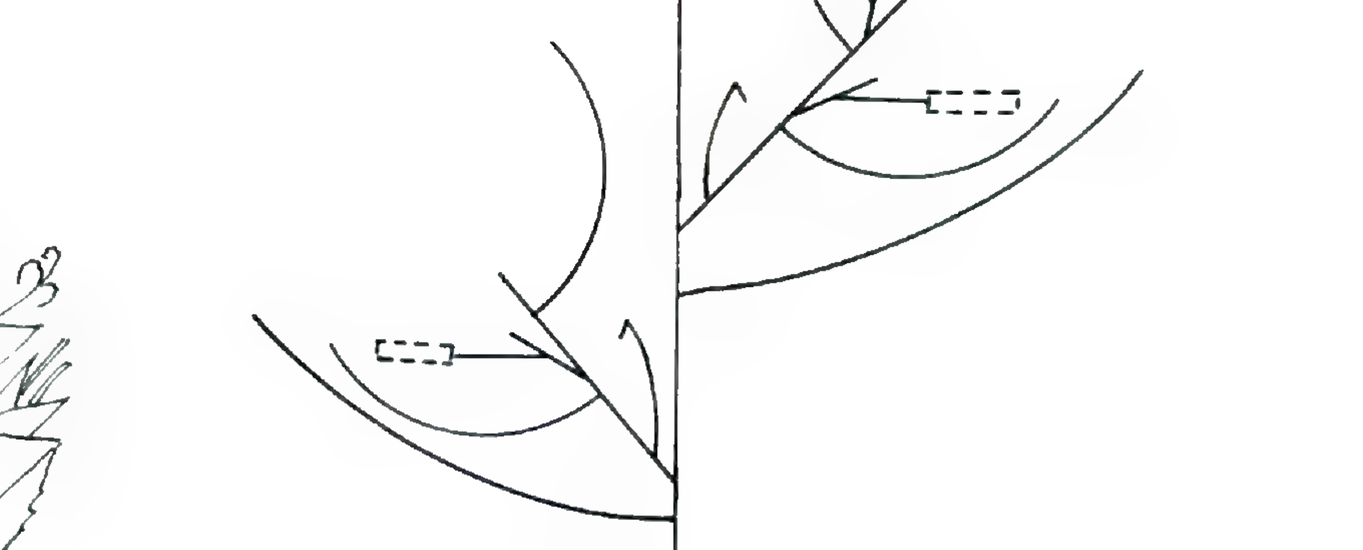
Figures 115–118.—115. Habit of a plant with two heads; × 0.4.—116. Pistil; × 19.—117. Fruit showing longitudinal grooves and basal cupule; × 19.—118. Fruit between its two apical free scales; × 8.

The internodes inside a head are very short, especially those inside a fascicle, so that the prophyll of an axis often appears to arise from the base of the adaxial surface of the subtending bract of that axis (Fig. 152). But while the bract arises from an axis of a certain branch order, the prophyll arises from the axis of the next higher branch order. The prophyll is a membranous laminule; on the lower-order axes it tends to be tubular in its basal part and surrounds the axis which bears it; on the higher-order axes the prophyll is open, flat and narrow.

On the lower internodes of a basal fascicle in a head where internodes are a few millimeters long, the prophyll visibly arises from its own axis separate from the subtending bract of that axis. But where the internodes are so short as not to be visible, it is necessary to use the order in which lateral organs arise, and to note which lateral organs are included in which others, in order to analyze the branching pattern. The presence of a morphologically distinct prophyll makes this possible.

The structure of each fascicle is very variable, those at the base of a head having more elements. The fascicle is composed of 2–3 naviculate outer bracts 4.0 mm long, each with a toothed winged keel. As will be seen, these outer bracts are the subtending bract of the whole fascicle (if this bract remains attached to the fascicle when it is pulled out of the head), and the subtending bracts of the lowest side branches of the fascicle. These outer bracts surround





FIGURES 119–122. Fascicle of three fusiform bodies.—119. Natural aspect; × 5. The central fusiform body is female and the two lateral ones are male spikelets. The two glumiform bracts which appear to surround the fascicle are really the subtending bracts of the male spikelets.—120. The same fascicle with the parts of the left fusiform body (male spikelet) spread out; × 5. From center to left in this spikelet, note prophyll (short scale), upper glume, lower glume with exserted filament, and the keeled glumiform bract which subtends the spikelet.—121. Branching pattern of this fascicle. The rectangles in dashed line represent fallen anthers, the hooked curves the prophylls. This branching pattern is the only one that has previously been described for the genus.—122. Floral diagram of this fascicle. The M-shaped symbols represent the prophylls, the dark points the rachilla apices. (In the branching pattern diagrams a lateral axis is shown slightly separated from the bract in whose axil it arises. This slight separation is of course not an internode since the bract and the axis arising from its axil come from the same node.)

2–6 flat "fusiform bodies"; each body moves as a whole when pushed by a needle. Each fusiform body is surrounded by 1–2 glumiform, winged, naviculate bracts. Filaments and stigmas extend beyond the apices of the fusiform bodies.

Several fascicles were extracted from various parts of single heads (Figs. 119, 123, 126–129, 135) and analyzed to determine the unit which could be considered the spikelet. A great variety of structures was found in the fascicles from heads

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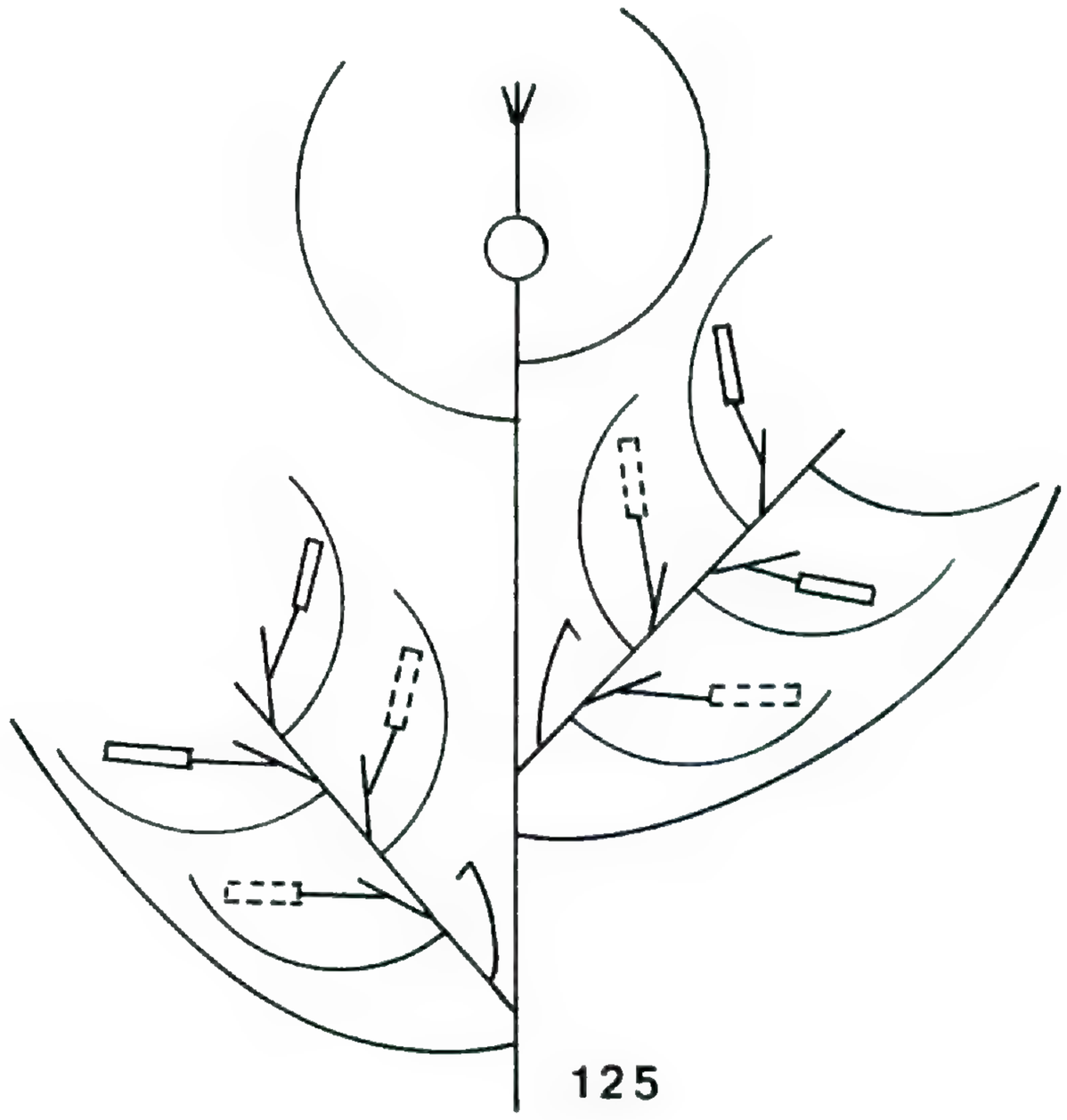

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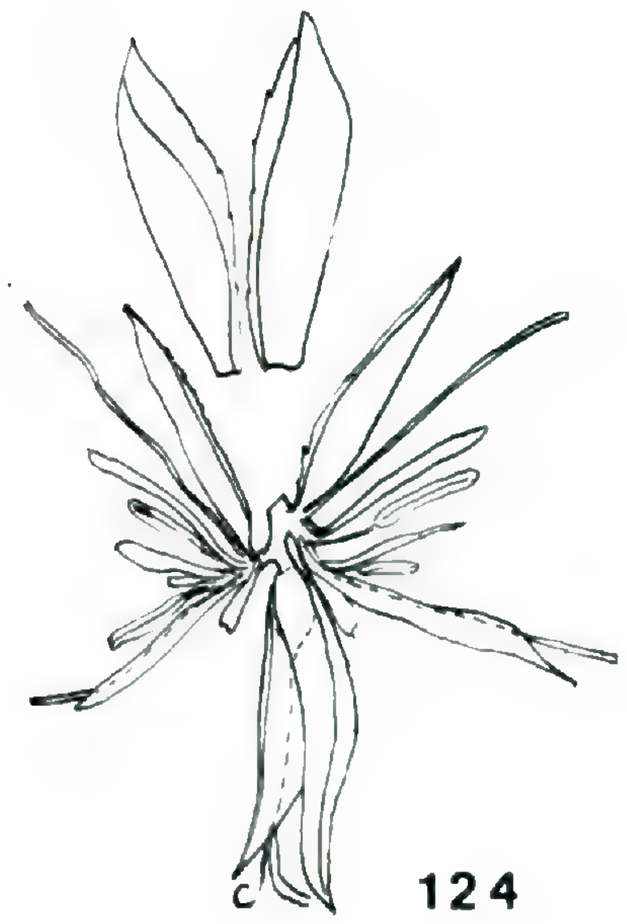

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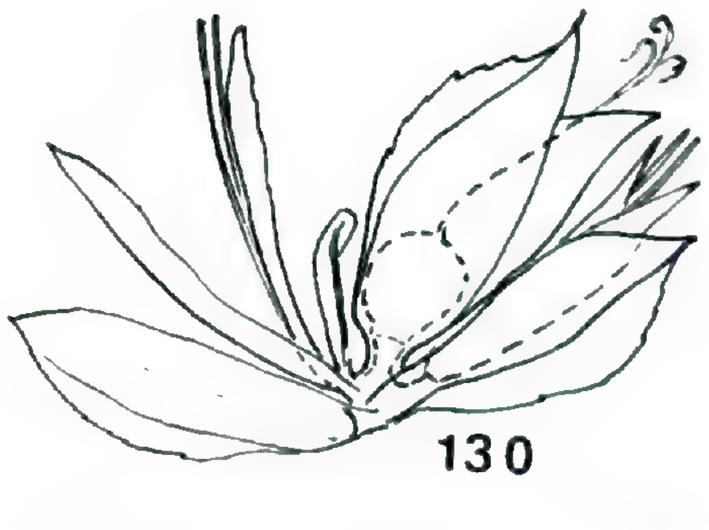

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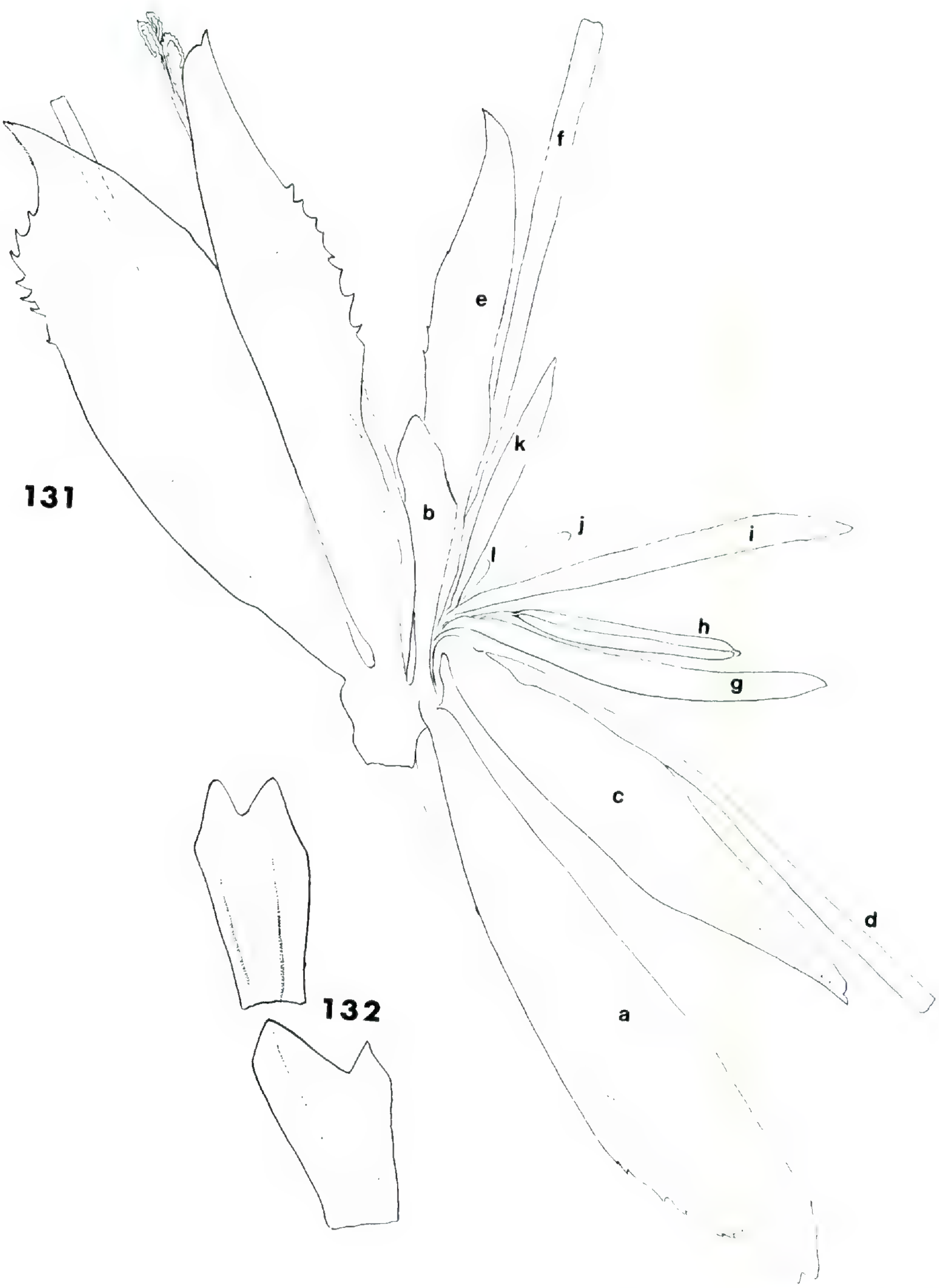
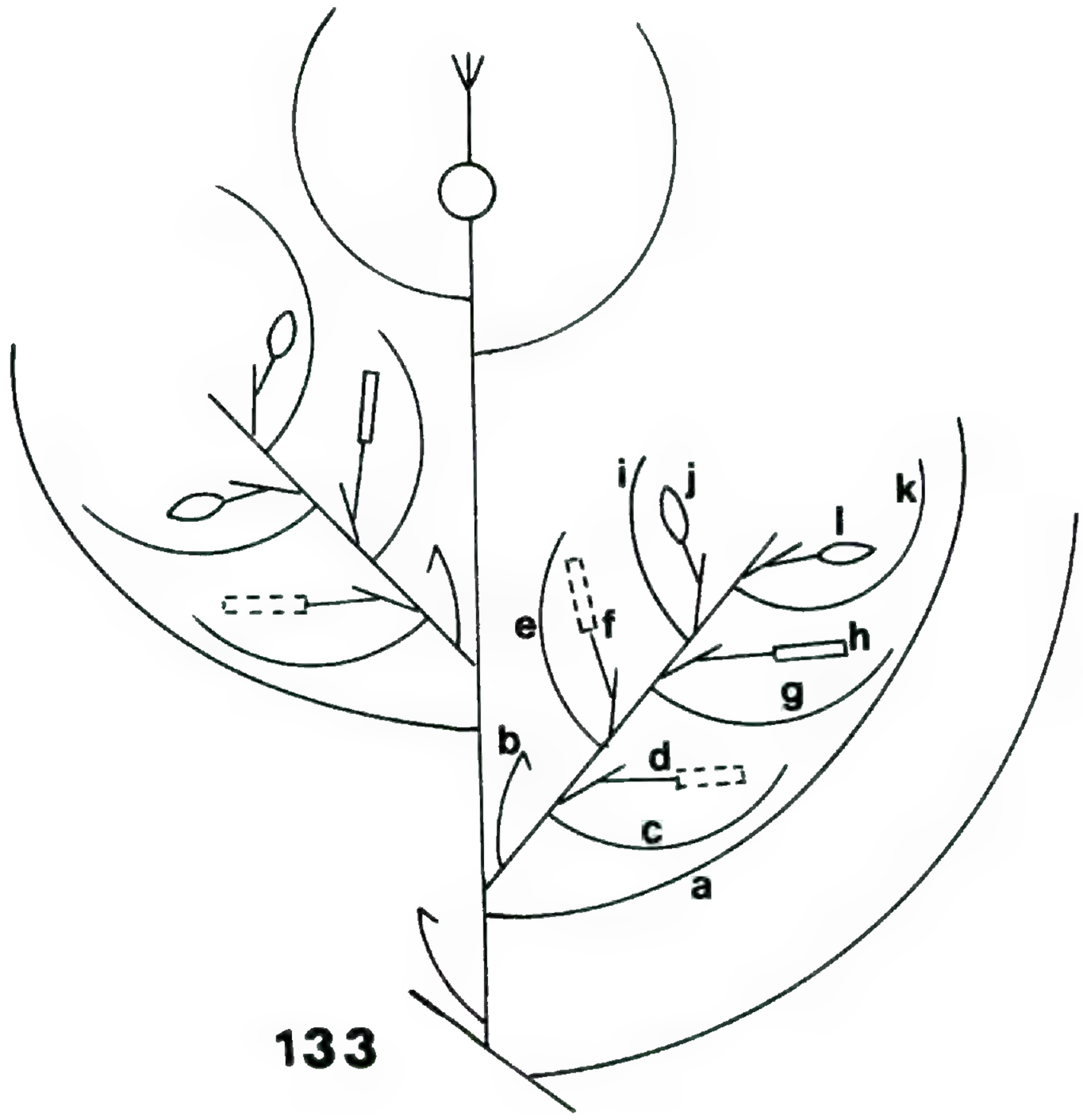
FIGURES 123–130. Fascicle types.—123. Natural aspect of a fascicle of three fusiform bodies, a central female and two lateral male bodies; × 5.—124. The same fascicle with the two keeled bracts removed (shown above, detached), and the parts of the two lateral fusiform bodies (male spikelets) spread out; × 5. The central fusiform body (containing the pistil) is here directed downwards.—125. Branching pattern of this fascicle. The rectangles in continuous line represent anthers which are present. The general pattern is the same as in Fig. 121.—126–130. Other fascicles of the same capitulum, showing variation in number of fusiform bodies; × 5.



FIGURES 131–132.—131. Fascicle with three fusiform bodies; that to the right has had its parts spread out; × 23. a = keeled glumiform bract which subtends the male spikelet; b = prophyll; c, e, g, i, k = glumes; d, f = filaments from which the anthers have fallen; h = stamen with mature anther; j, l = anthers of young stamens.—132. Dorsal view of two prophylls spread out, showing the retuse apex and two veins. (The prophyll of the fascicle as a whole, and the bract in whose axil it arose, shown in Figs. 133–134, are not shown in this figure.)



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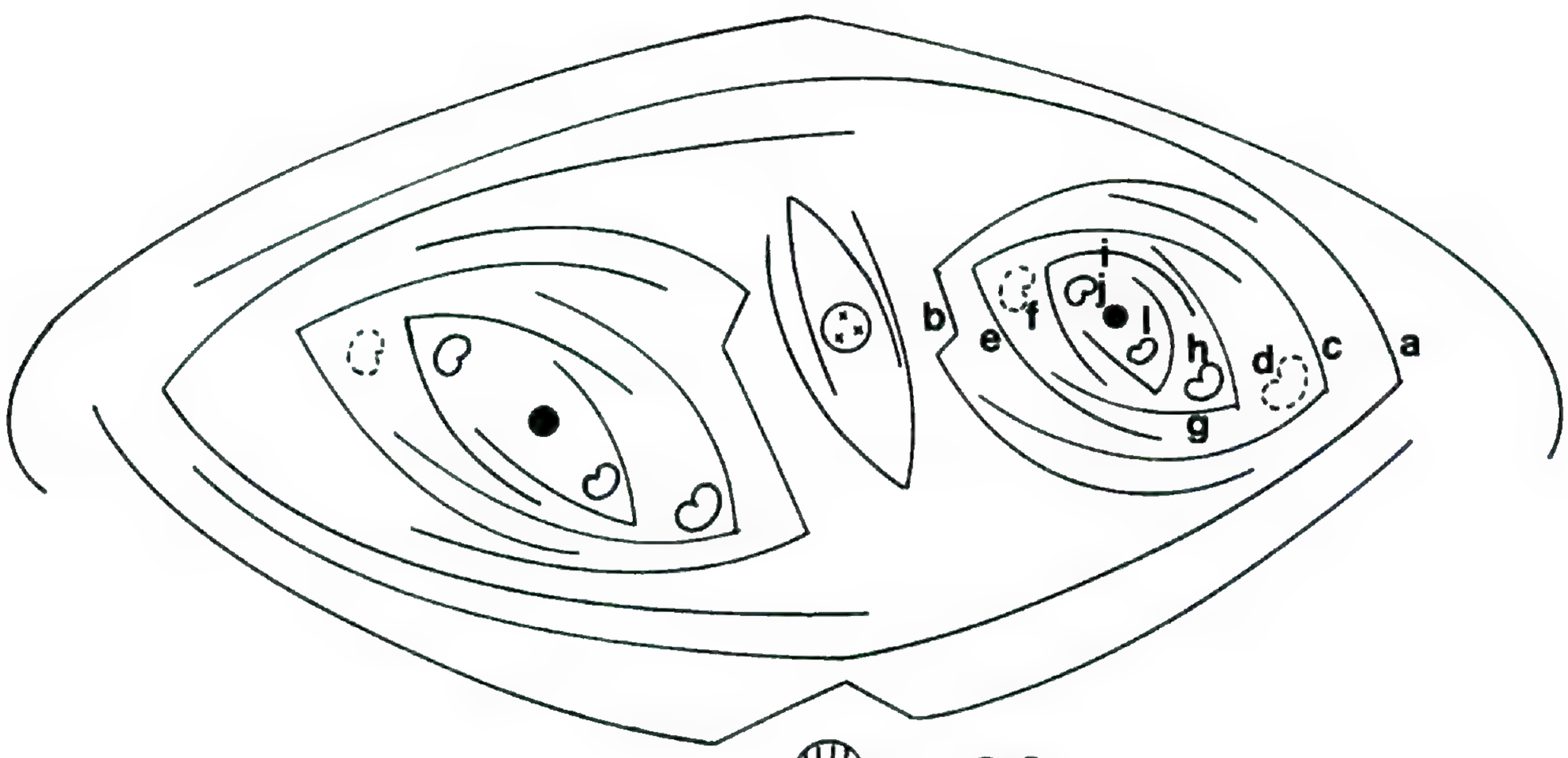

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Figures 133–134.—133. Branching pattern of fascicle shown in Fig. 131. The fusiform symbols represent immature anthers. The letters represent the same parts as in Fig. 131.—134. Floral diagram of the fascicle shown in Fig. 131. The shaded circle below represents the axis from which the fascicle arises laterally. The pistil apparently terminates the central axis of the fascicle.

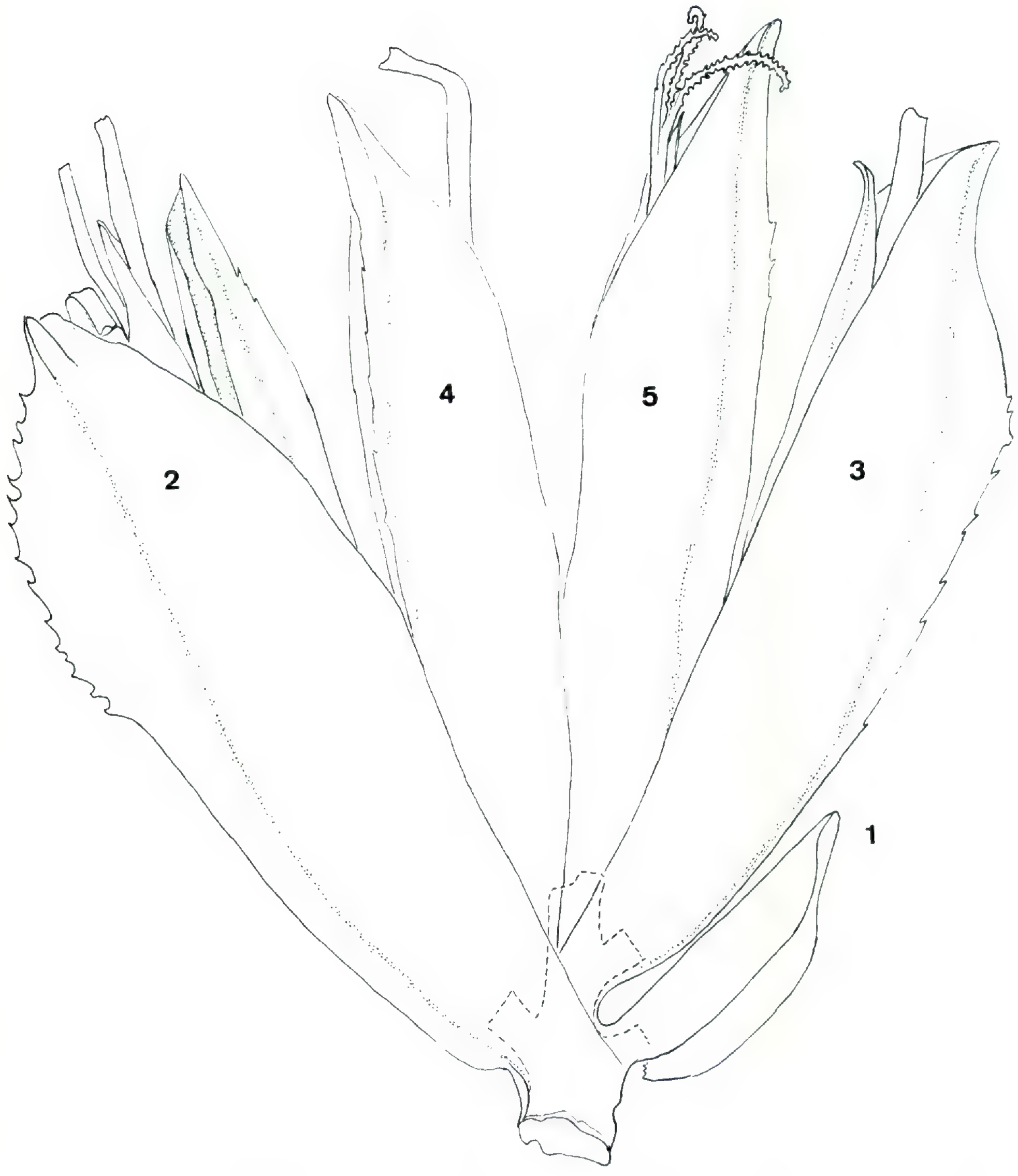
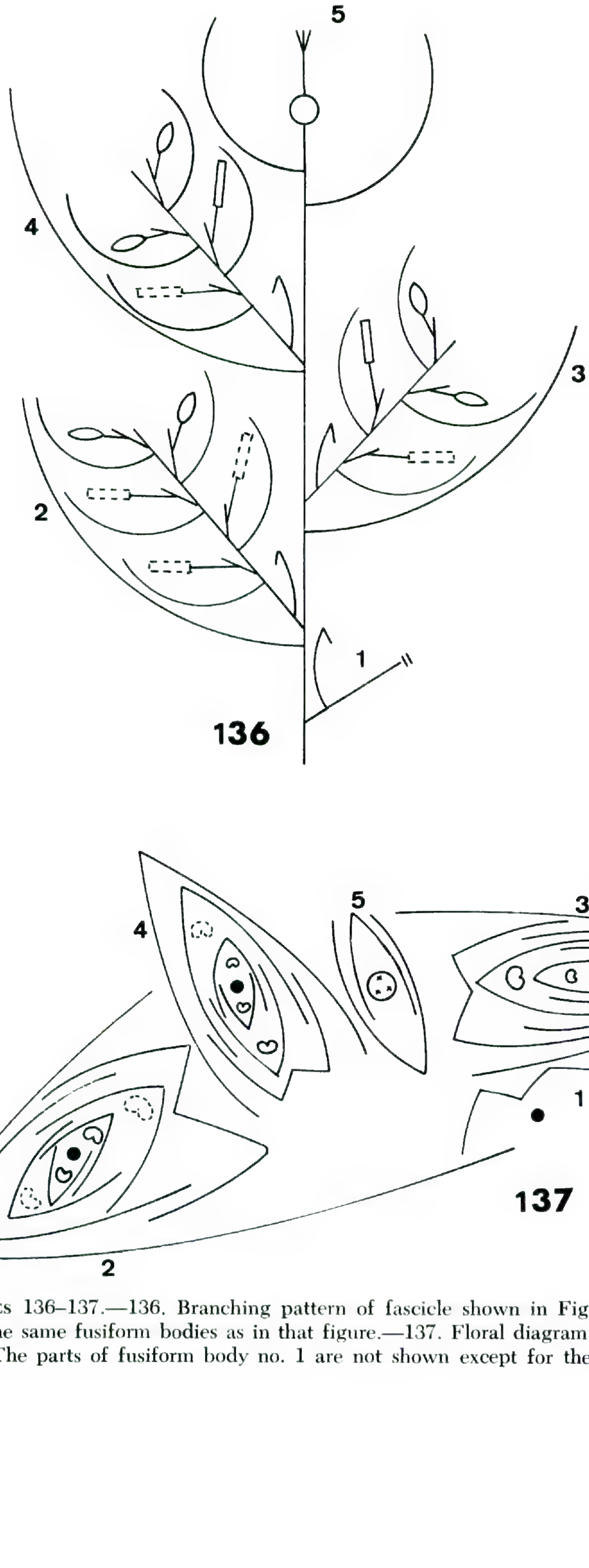
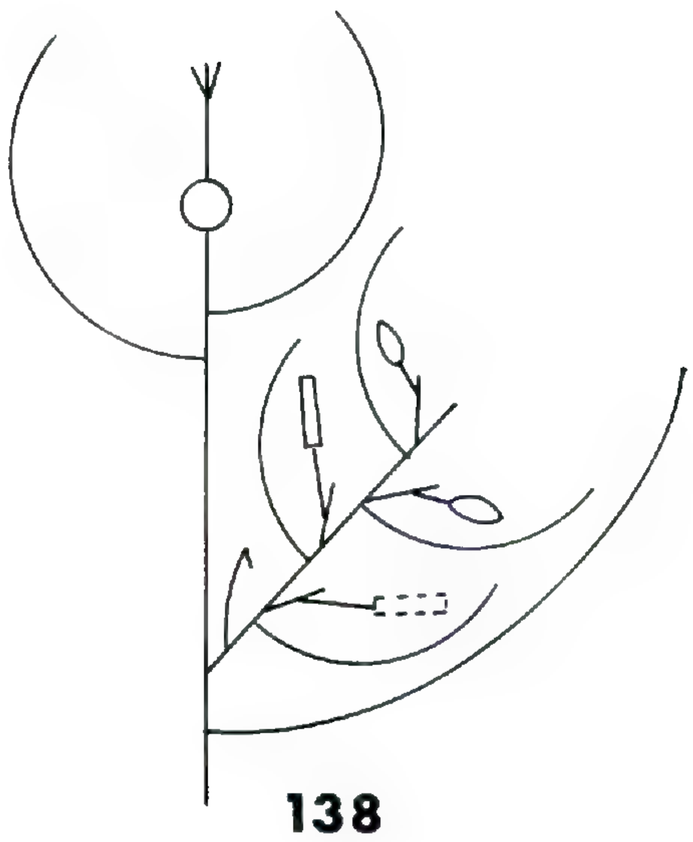


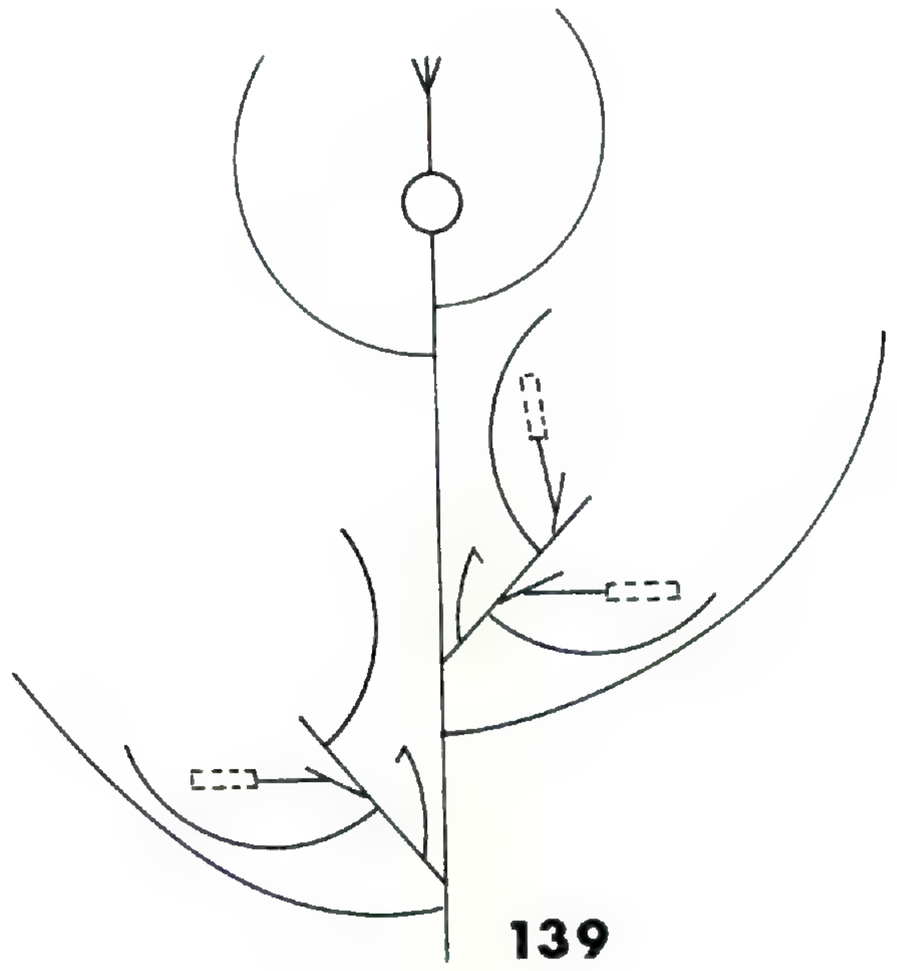
FIGURE 135. Natural aspect of a fascicle of five fusiform bodies; × 29. The fusiform body to the right (no. 1) and its subtending bract were removed; only its prophyll remains in this drawing. The axis of the fascicle and its branches (rachillae) are shown in dashed outline.

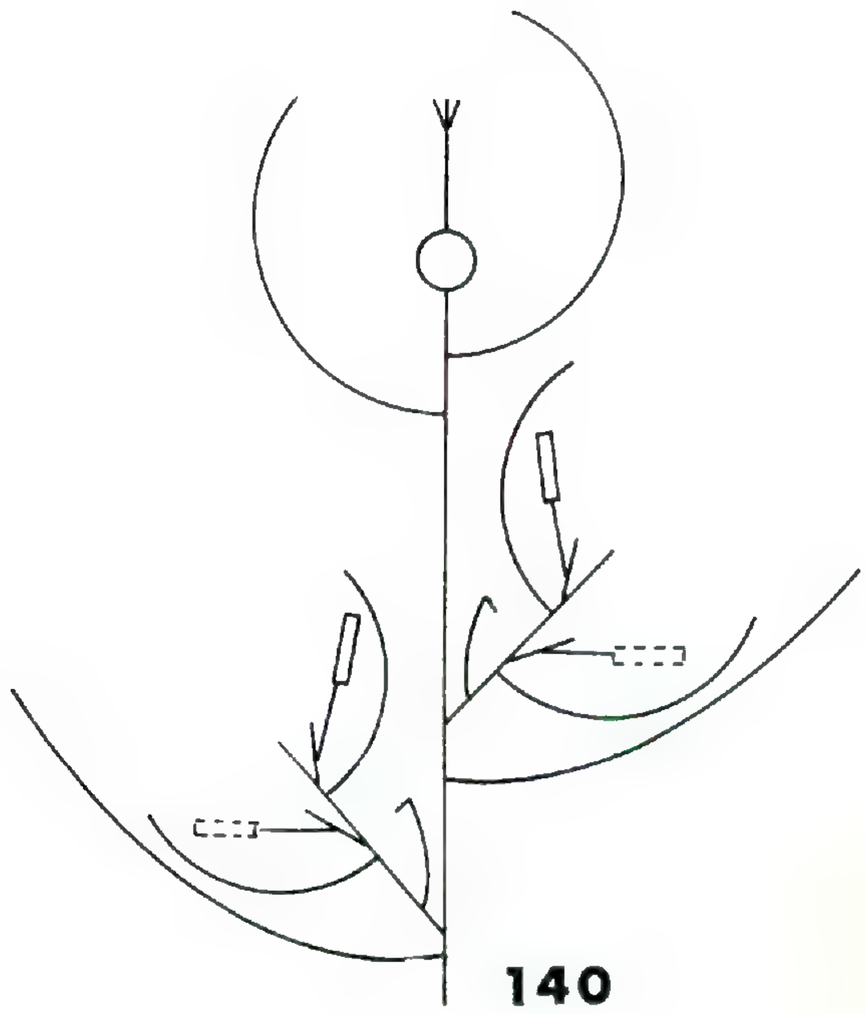
of the two collections when these were opened out and examined (Figs. 120, 124, 130–132, 152). The branching patterns found are given in Figs. 121, 125, 133, 136, 138–151. For a few of the fascicles the floral diagram is also given (Figs. 122, 134, 137, 153). Each bract, glume, scale, prophyll, stamen and pistil shown was actually seen. The internode lengths in these diagrams, as in all diagrams of branching pattern in this paper, are exaggerated for greater clarity, so as to show better to which axes the various parts are attached.

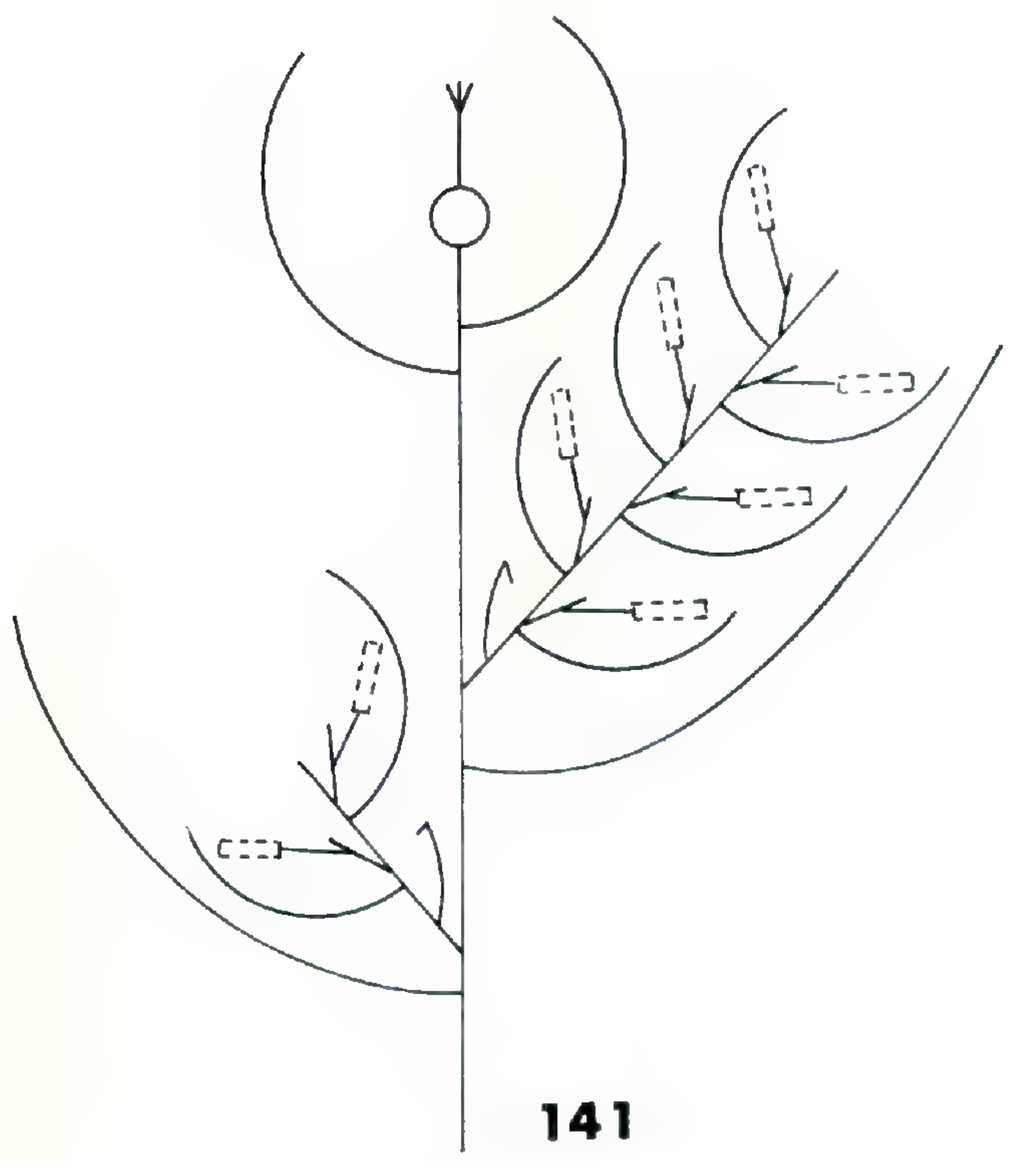


Figures 136–137.—136. Branching pattern of fascicle shown in Fig. 135. The numbers represent the same fusiform bodies as in that figure.—137. Floral diagram of fascicle shown in Fig. 135. The parts of fusiform body no. 1 are not shown except for the prophyll.









FIGURES 138–141. Branching patterns of other fascicles examined.—138. Fascicle of two fusiform bodies: one female made up of a pistil and its two free scales, and one male which is a spikelet of male monandric flowers with its prophyll and subtending bract.—139–141. Fascicles of three fusiform bodies: one central female and two lateral males. Note variation in stamen (i.e., male flower) number.

In general, a fascicle has a central axis which arises in the axil of a bract (the bract is glumiform in the distal fascicles in a head), a small membranous prophyll (almost imperceptible in the distal fascicles) as its basal lateral organ, 1–4 side branches, and at the apex two free, winged, naviculate scales surround-

ing a pistil. Each side branch from the central axis arises in the axil of a glumiform bract and possesses a prophyll. The parts which these side branches bear vary in nature and number. The following structures were found making up the side branches: (1) single axis with prophyll and 1–9 glumes, each glume subtending a male flower of a single stamen or sometimes the distal glume empty (Figs. 121, 125, 133, 136, 138–148, 149 upper left side axis); (2) single axis with 2 or 4 scales, the two basal ones (when there are four) are empty and the two distal ones are always free (not fused by their edges) and surround an apparently terminal pistil (lowest side branch in Figs. 142–143, 145; lowest two side branches in Figs. 146–148); (3) a side axis which itself is branched. In these, the side axis terminates in a pistil surrounded by two scales; each of its own 1–2 lateral branch axes arises in the axil of a bracteole and has a prophyll and 1–2 glumes, with each of these glumes subtending a male flower of one stamen, or the upper empty (the two lower side branches in Fig. 149; lower side branch in Fig. 150; both side branches in Fig. 151).

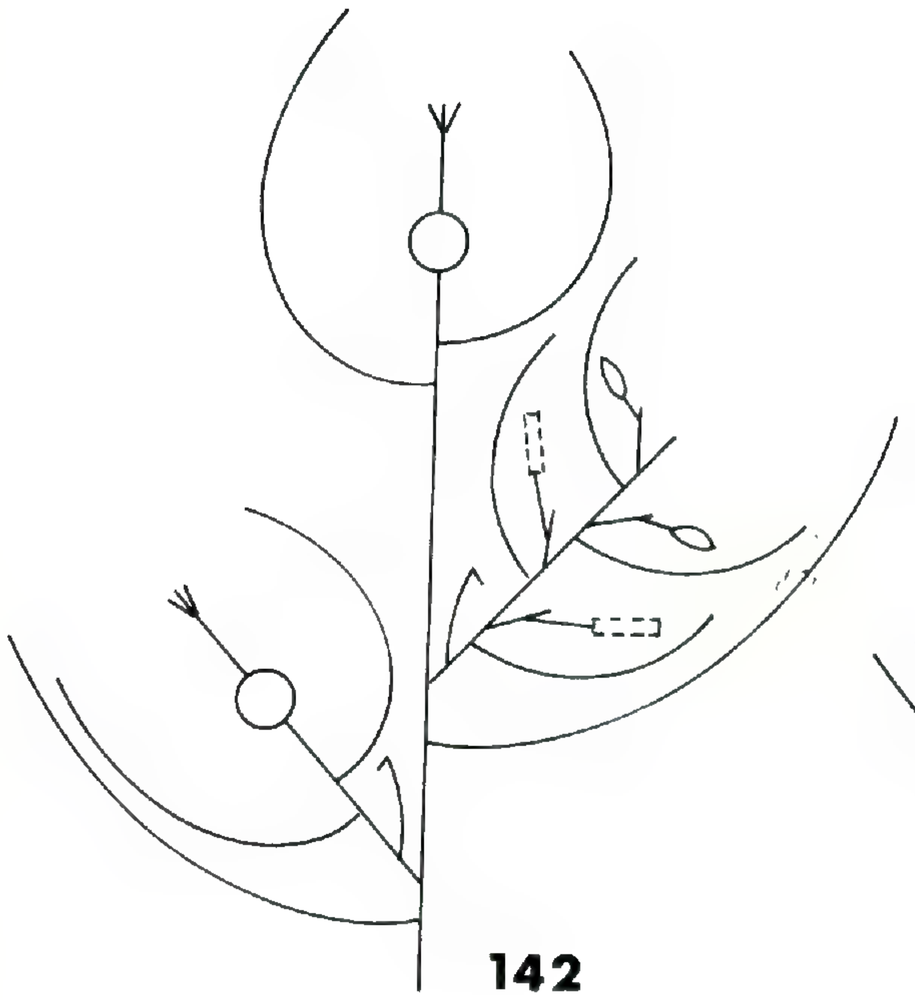
I consider a "spikelet" a structure composed of a single axis of theoretically indefinite growth, bearing lateral sessile flowers in the axils of bracts called "glumes." In the plant here studied, the structures containing the male flowers are clearly spikelets. I do not include the subtending bract or the prophyll in the definition of the spikelet. The axis bearing the pistil is apparently of definite growth since the pistil appears to be terminal and I have indicated this in the branching pattern diagrams. I believe, however, that all flowers in the Cyperaceae are fundamentally lateral and that those that appear terminal on the rachilla are really only pseudoterminal, as is clearly true in 1-flowered spikelets of *Cyperus* (sensu lato), *Eleocharis*, etc. But until I have direct proof or at least an indication that the pistil in *Bisboeckelera* and *Diplacrum* is really lateral, I do not wish to consider this terminal portion of the axis with its scales and pistil a spikelet. I use the term "scale" here since I reserve the term "glume" for the lateral laminar organs of what I consider a true spikelet.

In three cases seen, the central axis of the fascicle did not terminate in a pistil but merely stopped, and just below its tip gave rise to two lateral branches, each arising in the axil of a keeled bract and provided with a prophyll at its base. These branches were either simple and terminated in a pistil with its two scales (Fig. 150, upper side branch), or were compound with 1–2 lateral basal branch axes arising in the axils of bracteoles and possessing a prophyll, glumes and male flowers of one stamen each (Fig. 150, lower side branch; 151, both side branches).

Of 18 fascicles analyzed, in 10 the central axis was wholly contained in the fascicle, that is, the prophyll of that axis and its subtending bract had separated from the inflorescence as part of the fascicle. In the remaining 8 cases the fascicle contained only the upper part of the main axis; its base remained with the rest of the head so that its prophyll and subtending bract were not found in the detached fascicle.

This analysis showed:

1. All axes of the inflorescence arise in the axils of bracts and have a prophyll as the first basal lateral organ.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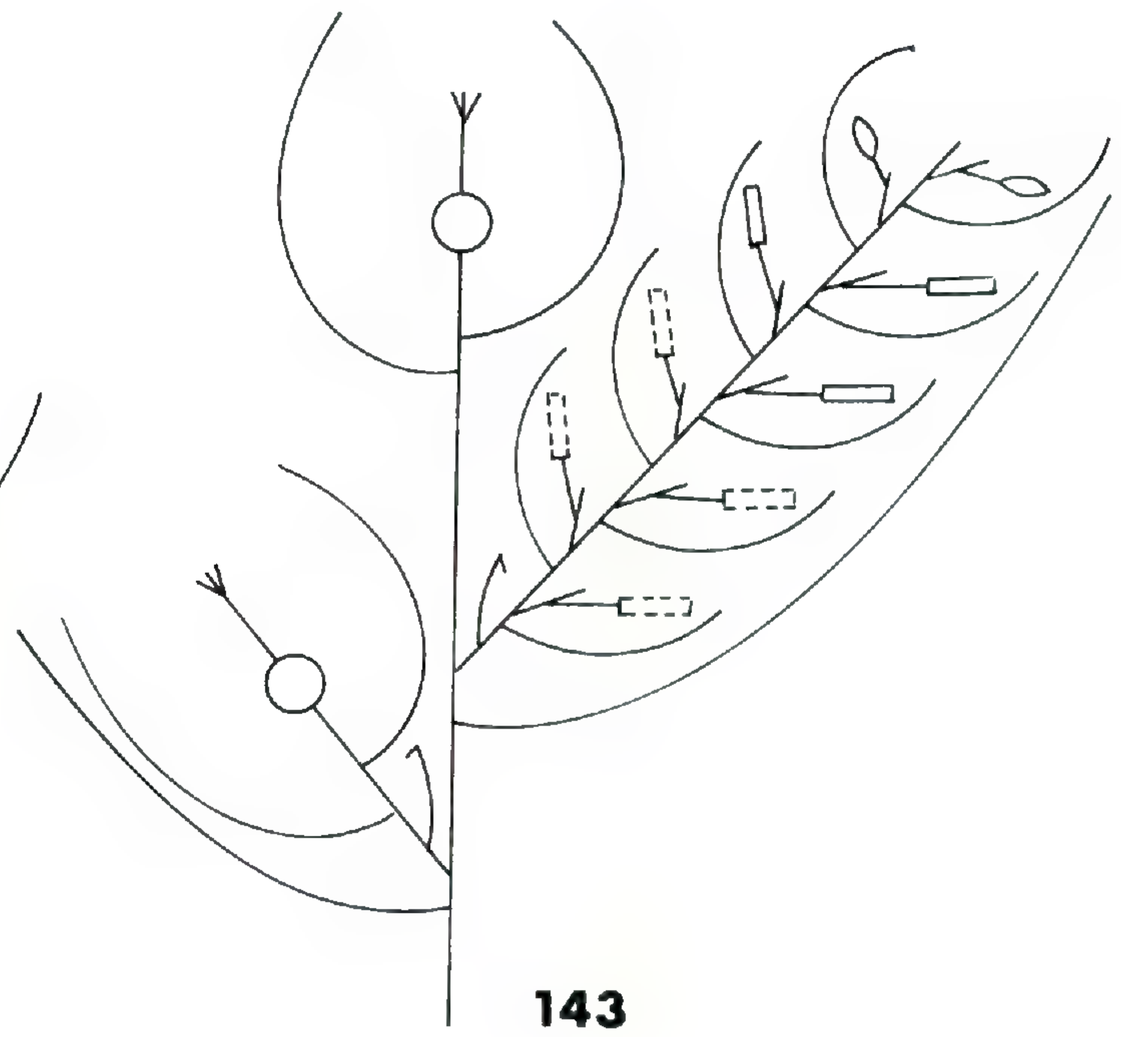
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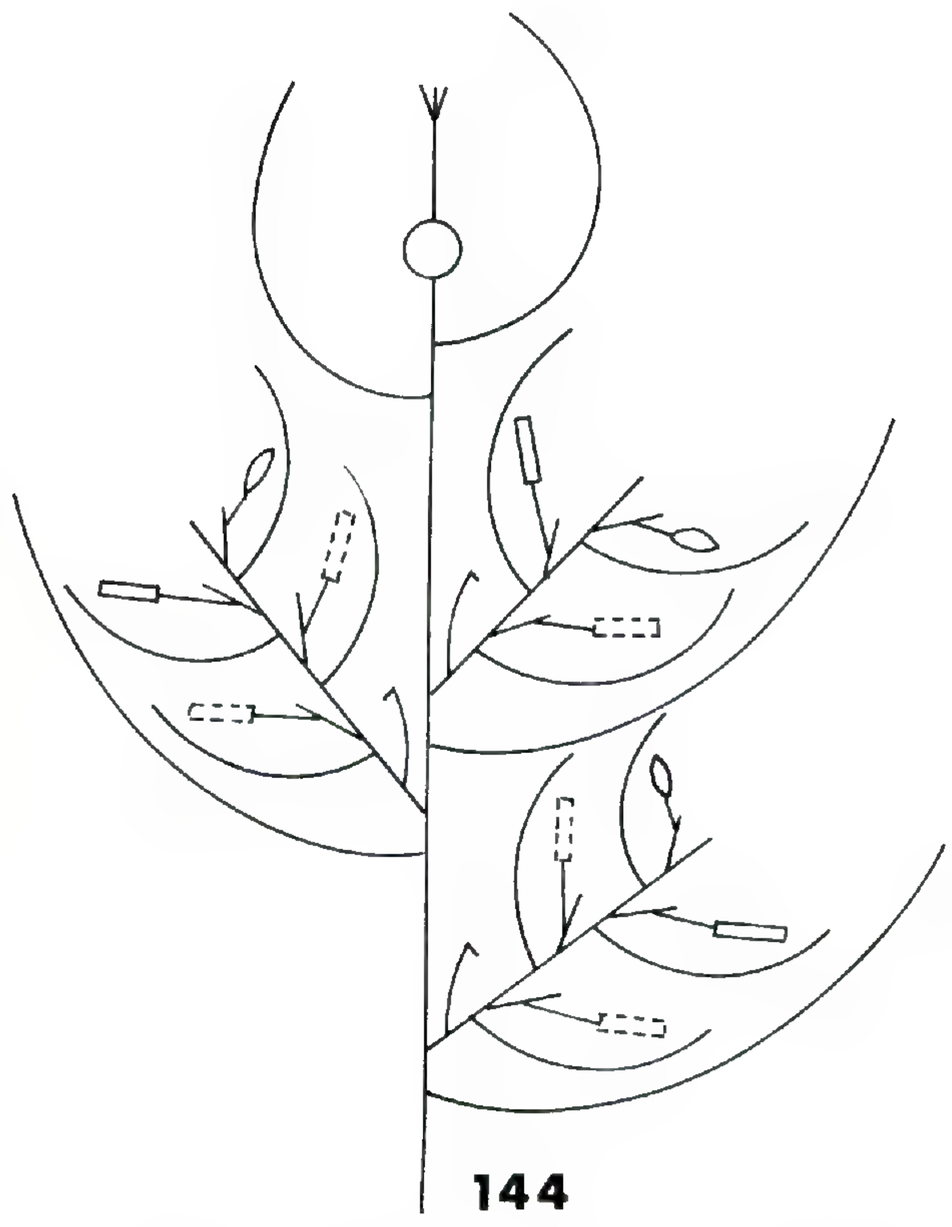
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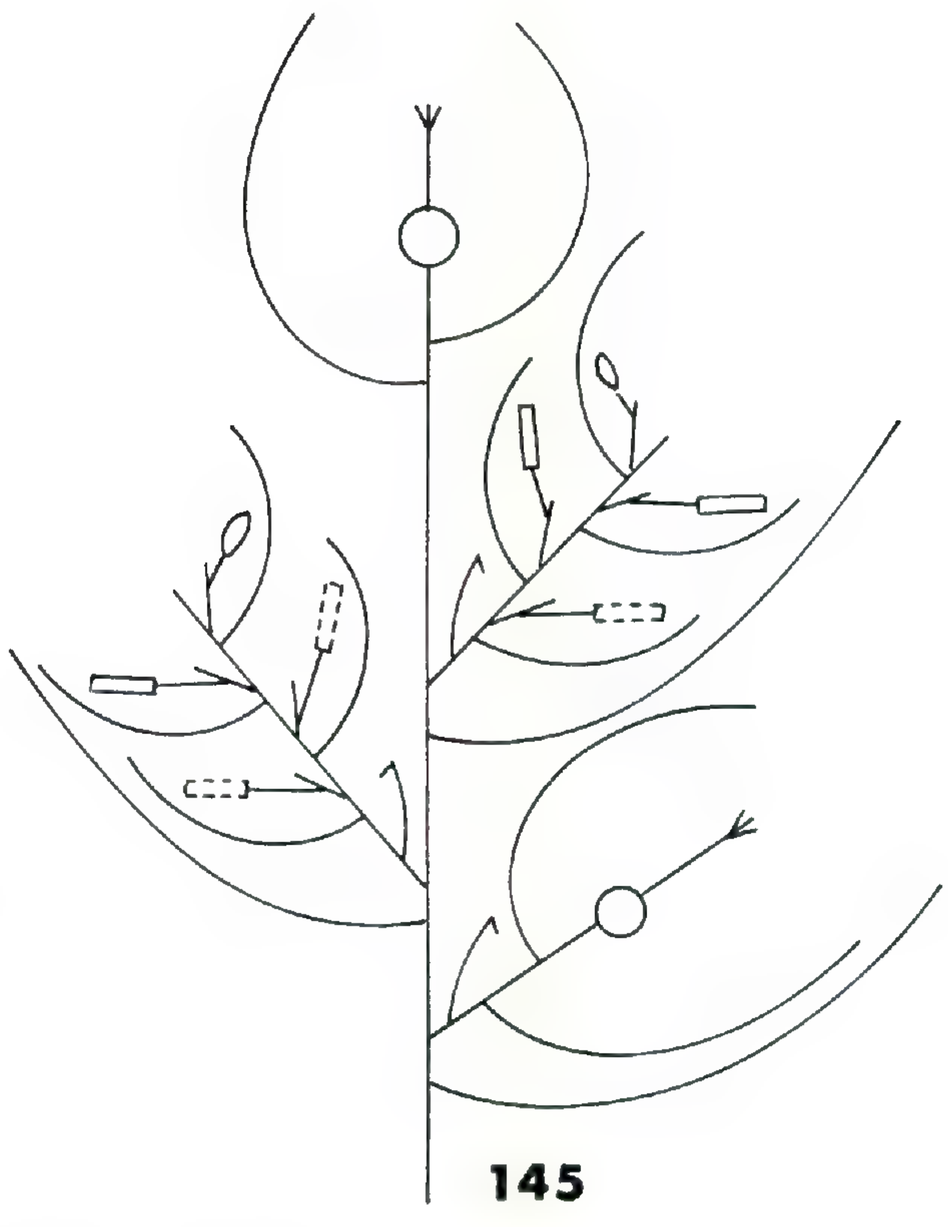
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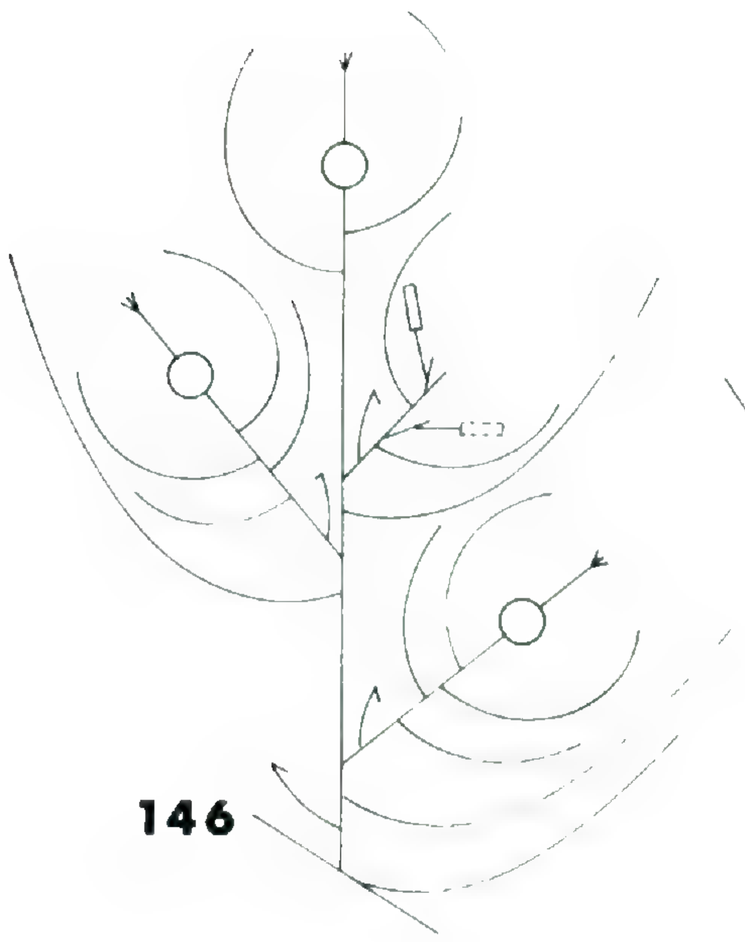
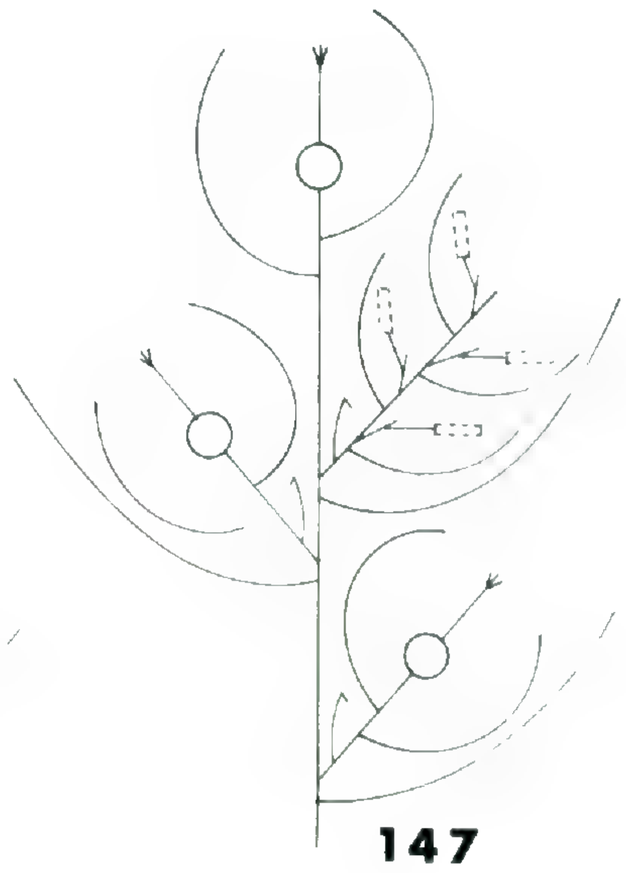
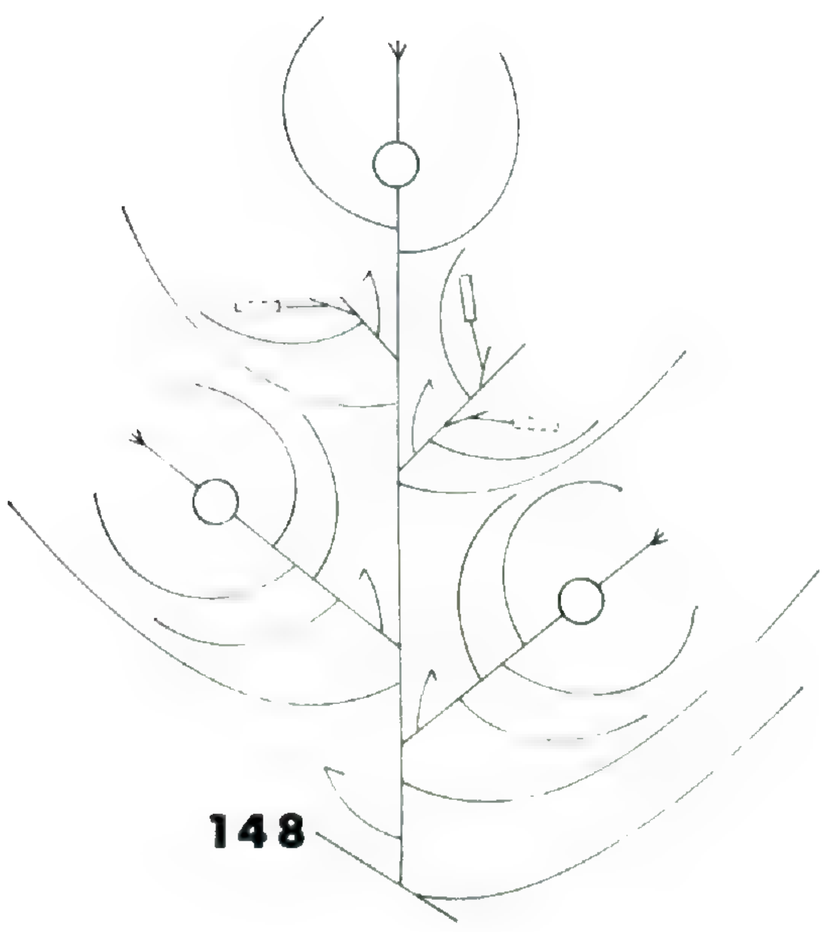
FIGURES 142–145.—142–143. Fascicles of three fusiform bodies: one central female and two laterals of which one is female and the other male.—144. Fascicle of four fusiform bodies: one central female and three lateral males.—145. Fascicle of four fusiform bodies: one central female, two lateral males, and one lateral female.

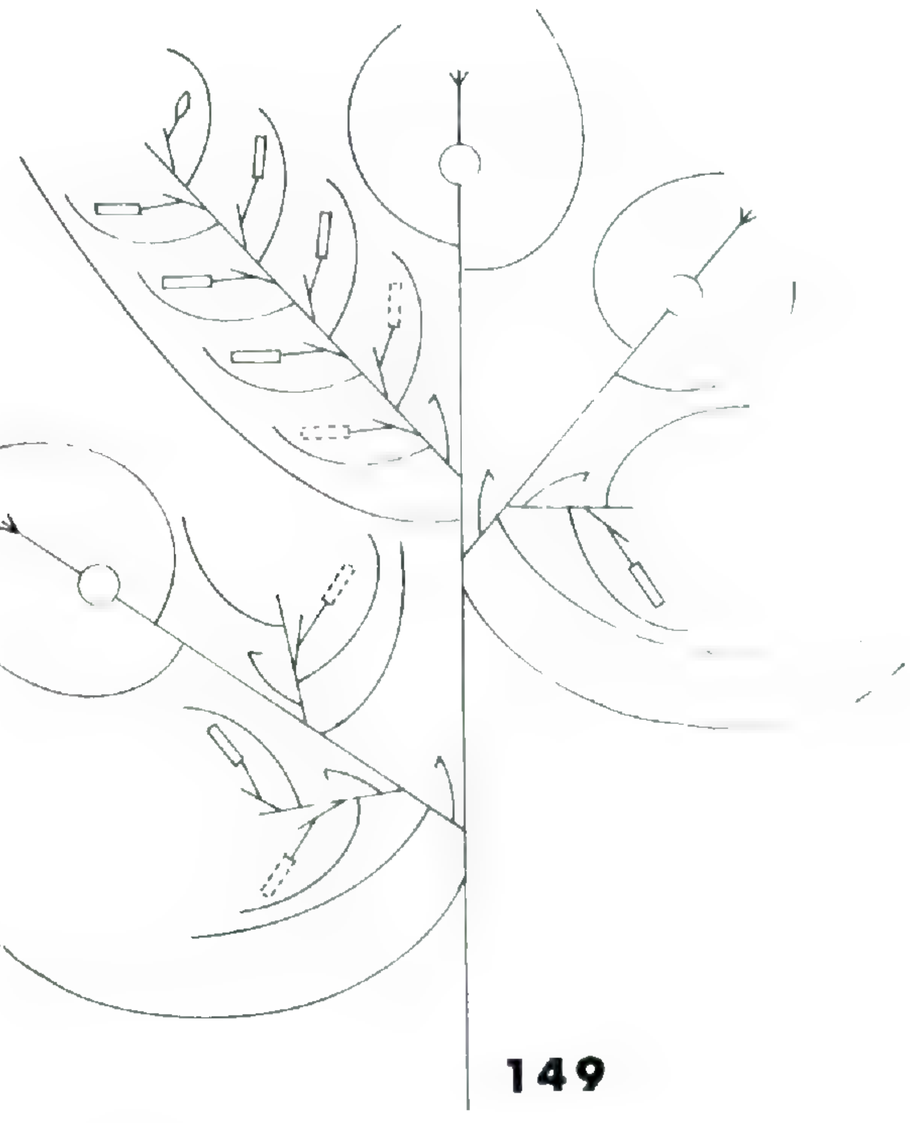
2. The ends of the branches of the inflorescence, that is, those axes which do not branch anymore, form the rachillas of spikelets of 1–9 single-stamen male flowers, or bear 2 or 4 scales and apparently terminate in a pistil.

3. All the scales are free, including the two which surround the pistil. There





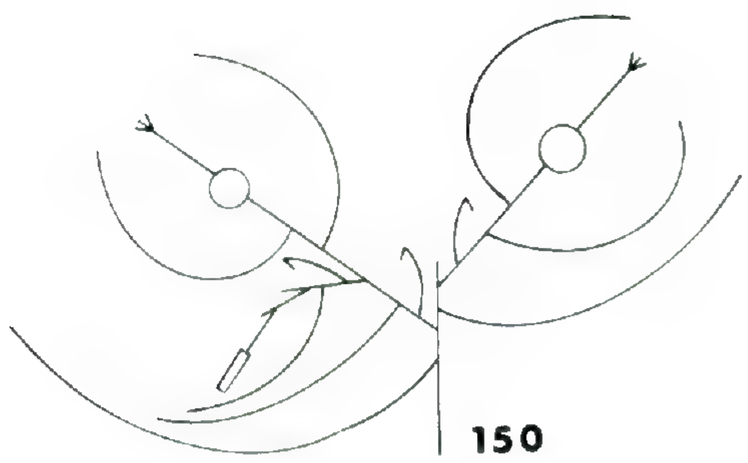


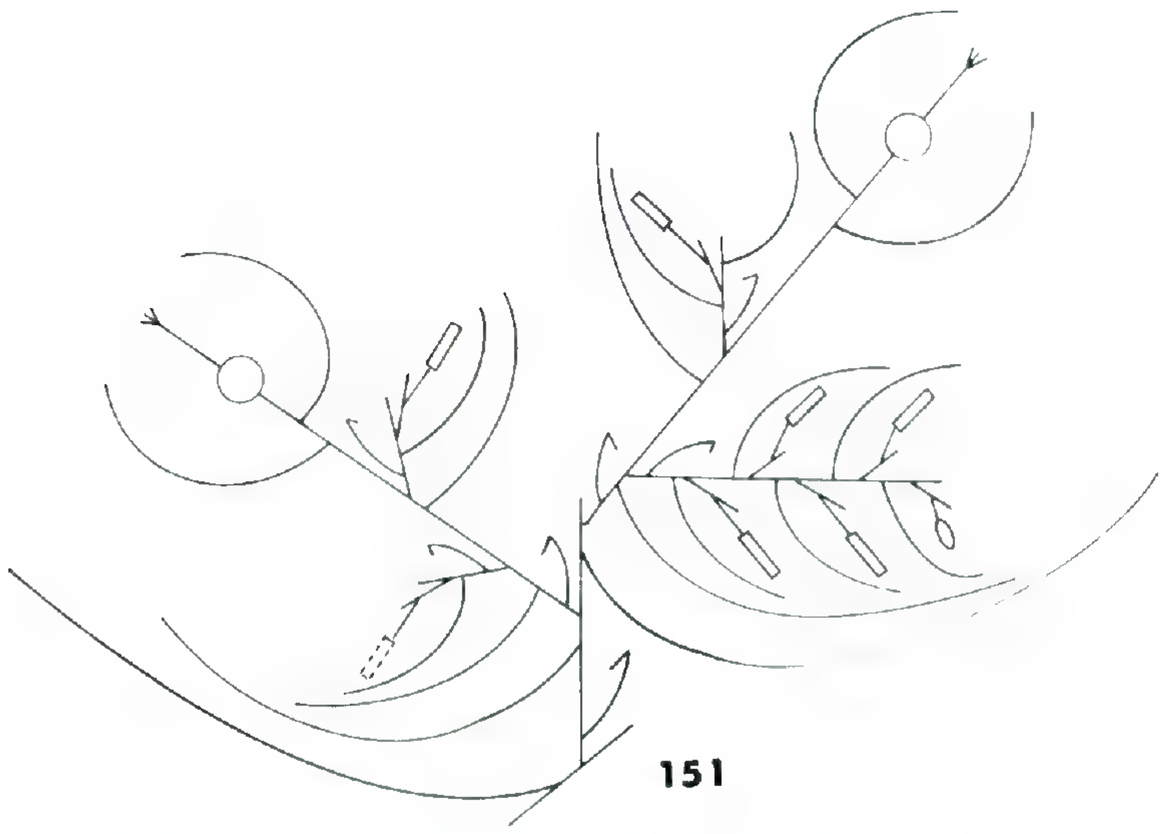


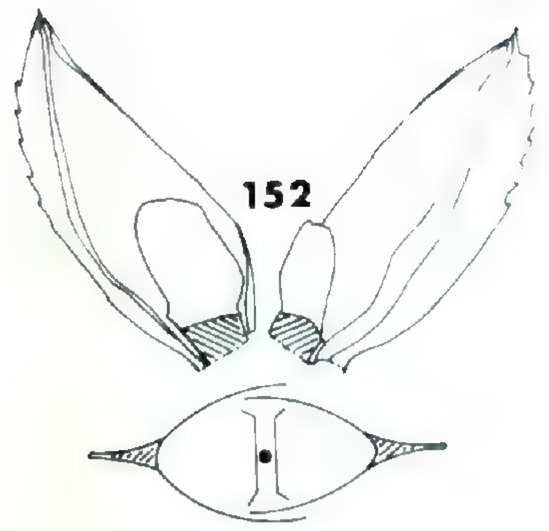
FIGURES 146–149. Fascicles of four fusiform bodies.—146–147. Fascicles with one central female, one lateral male and two lateral female bodies. Note that the lateral female bodies may have two or four scales.—148. In this fascicle the central fusiform body is bisexual since it is made up of the pistil on the central axis and its two scales *plus* the most distal lateral male spikelet of one flower and its prophyll and subtending bract. Each of the other three lateral branches forms a separate fusiform body.—149. Fascicle with one central female, one lateral male (a many-flowered spikelet), and two lateral bisexual fusiform bodies. The latter two are themselves branched, the branches being reduced male spikelets.

is no formation of a utricle even though the two scales which cover the pistil arise at almost the same level.

4. The ultimate "units" of the inflorescence, made up of axes of the last few branch orders and the lateral organs they bear, can only be delimited based on the branching pattern, not based on spatial individuality. For example, the "fusiform bodies," which are the smallest units more or less spatially distinct one







FIGURES 150–153. Fascicles without a central terminal female fusiform body, only two lateral bodies.—150. Branching pattern with one body female and one bisexual.—151. Branching pattern with both lateral bodies bisexual.—152. Fascicle with the upper part of the two lateral branches removed and the central axis split; × 6. The two keeled subtending bracts of the branches and their prophylls are shown. The prophylls arise from an axis of higher order than that from which the subtending bracts arise (see Figs. 150–151).—153. Cross section of this fascicle.

from the other, cannot be considered the ultimate units of the inflorescence. The organization of a fusiform body is very variable; its axis may be simple or itself branched and the number of pistils and male spikelets it contains is not constant.

5. It is of course possible to define only two types of ultimate inflorescence units in this genus: (a) a male unit consisting of a male spikelet, and, if one wishes, also the prophyll and subtending bract, and (b) a female unit consisting of the tip of an axis with a pistil and the two scales below it. (When there are four scales below the pistil, the lower two should not be considered part of this female unit since in many cases, such as those shown in Figs. 149 and 151, these two lower scales subtend male spikelets.) However, traditionally, the "spikelet" of *Diplacrum* in taxonomic descriptions includes both the male and female parts. The description given here shows how much this can vary in even one head.

After having examined the inflorescence units and the vegetative characters of *Luetzelburg 23981* and *23955*, I can state with confidence that these collections are *Diplacrum longifolium* (Griseb.) Clarke and not a new species of *Bisboeckelera* as Süssenguth thought. In *Bisboeckelera* the female flower is always inside

a utricle while in *Diplacrum* the scales that surround the pistil are free and do not form a utricle. Thus, *Bisboeckelera paporiensis* is a synonym of *Diplacrum longifolium*. Koyama (1967) also noted this synonymy but did not give the reasons to justify his decision.

Süssenguth (1943) called the *spikelets* of male flowers with one stamen a "male flower." Probably he examined only one spikelet with three stamens for he wrote: "Flor masculus tristaminatus."

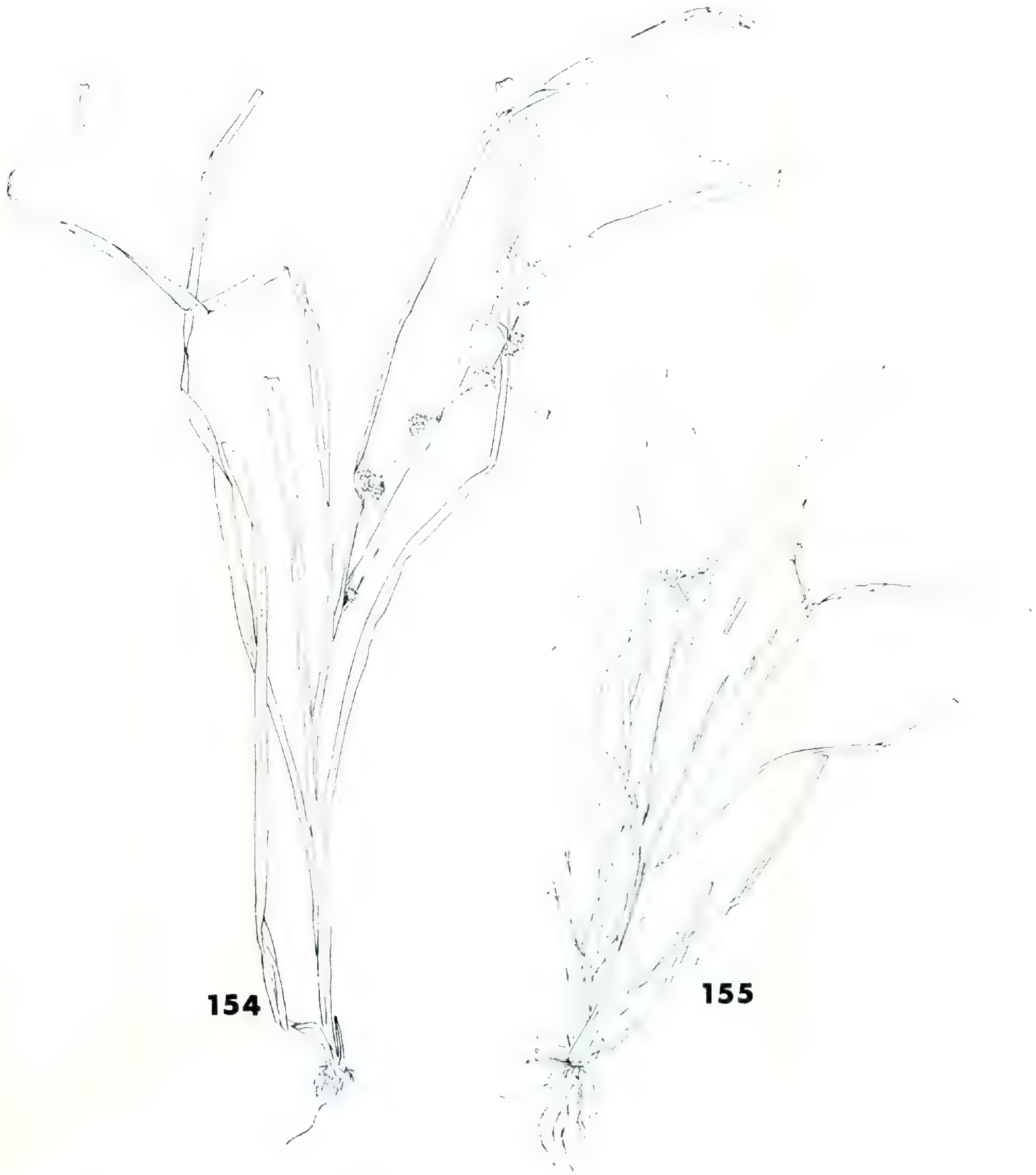
It is strange that Süssenguth did not see that this material belongs to the genus *Diplacrum*. He thought it similar to *Bisboeckelera* and compared the specimens to the illustration of *Hoppia irrigua* Nees (= *Bisboeckelera irrigua* (Nees) O. Ktze) in Plate 136 of Clarke (1909). He saw that the specimens were not *B. irrigua* because of the absence of a utricle and because the leaves in the specimens were much narrower. Plates 134 and 135 of this same book of Clarke are species of *Diplacrum* but these were not cited by Süssenguth. The "spikelet" of *Diplacrum longifolium* illustrated in Plate 135 is identical to that described by Süssenguth for *Bisboeckelera paporiensis*. But he did not recognize that Luetzelburg's collections were of the same species as the plant in Plate 135, probably because the Luetzelburg plants have only 1–2 small heads per flowering culm while the plant in Plate 135 is more robust with 4 large heads per culm.

Certain that his specimens belonged to *Bisboeckelera*, Süssenguth described the new species *B. paporiensis*, and established for this species a new section of the genus, *Bibractearia*, to contain species of the genus having the pistil enclosed in two free scales and not in a utricle.

Koyama (1967) recorded only two species of *Diplacrum* for the New World, *D. capitatum* (Willd.) Boeck., widely distributed in the tropical region, and *D. guianensis* (Nees) Koyama of southern Venezuela and the Guianas. These two species are easily separable by the surface texture and color of the fruits and by the size of the keeled glumiform bracts. Koyama & Oldenburger (1971) registered the presence of the very different looking *Diplacrum africanum* Clarke in Surinam. In 1965 I had also noted this species in Brazil (Amapá, perto da cidade de Amapá, 29 Aug. 1955, *Black 55-18535*. Maranhão, perto de Carolina, campo cerrado, 26 May 1950, *Pires & Black 2247*), although I did not publish on it. In fact, Gross had previously annotated the Pires & Black collection as this species. In his monograph of the American species, Koyama used the name *D. capitatum* (Willd.) Boeck. instead of *D. longifolium* (Griseb.) Clarke, because the epithet *capitata* is older. However, I prefer to continue using *longifolium*, the epithet accepted by all cyperologists, until the type of *Scleria capitata* is identified beyond all doubt.

Besides Luetzelburg's two collections, I have studied 13 more collections of *D. longifolium* from Venezuela and Brazil. Even this small number was enough to show great variation in the characters usually used to separate species and varieties in this complex (Figs. 154–155). The following characters may be noted:

Number of heads per culm, 1–7; width of leaves, 1.5–10.7 mm; width of keel (wing) of the scales which enclose the fruit, 0.2–1.3 mm; length of basal leaves,



FIGURES 154–155. Habits of plants of other collections of *Diplacrum longifolium* (Griseb.) Clarke showing variation in number of capitula per culm; × 0.3.—154. *Ule 7671*, culm with seven capitula.—155. *Pires et al. 6305*, with 1–2 capitula per culm. This collection has a habit similar to the types of *Bisboeckelera paporiensis*.

22–70 cm; length of the basal bract of the inflorescence (cauline leaf), from (5.5–)22 cm to more than 60 cm; surface of mature fruit smooth, lightly wrinkled, or heavily wrinkled.

The correlation of characters is not sufficiently high among the collections studied, and there are no gaps in the variation pattern, so that it is not possible to divide the complex into species or varieties. Also, there is no correlation between the morphology and the geography.

Other collections studied (det. L. T. Eiten):
Diplacrum longifolium (Griseb.) Clarke
VENEZUELA. AMAZONAS: Río Atabapo (Río Orinoco), Cano Teni, 18 Oct. 1950, *Maguire* 29275 (IAN).

BRAZIL. AMAPÁ: Calçoene, 21 Aug. 1962, *Cavalcante* 52562 (IAN). PARÁ: Belém, 27–30 June 1944, *Baldwin Jr. 4542* (IAN). Belém, Buçuguara, 14 Oct. 1945, *Pires & Black 410* (IAN). Rio Moju, Fábrica, 31 May 1954, *Black 54-16257* (IAN). Colares, 29 Sep. 1954, *Black* s.*n.* (IAN). Região de Anapu, Rio Tapacu, Portel, 10 May 1956, *Fróes 32785* (IAN). Serra do Cachimbo, 425 m, 15 Dec. 1956, *Pires et al. 6305* (IAN). Região de Ariramba, mata a leste do acampamento do Jamacuru, 2 June 1957, *Black et al. 57-19843* (IAN). RORAIMA: Rio Branco pr. Serra Pelada, Oct. 1908, *Ule 7671* (IAN). AMAZONAS: Manaus, Flores, June 1910, *Ule 8817* (IAN). GOIÁS: Varedão do Relâmpago, duas léguas de Carolina, 28 May 1950, *Pires & Black 2394* (IAN). SÃO PAULO: Campo de Itirapina, 24 Jan. 1951, *Black 51-11317* (IAN).

MICROPAPYRUS VIVIPAROIDES Süss.

Description of holotype of *Micropapyrus viviparoides* Süss., Bot. Jahrb. Syst. 73: 116–117. 1943: Brasilia septentrionalis, Civitas Alta Amazonas, Rio Negro, San Felippe, sandiger Ufer in Urwald, 16 Oct. 1928 *Luetzelburg 22381* (M).

The plant is delicate, forms clumps 16–22 cm tall with several erect leafless cylindrical or slightly flattened culms (peduncles) 6–17 cm long and 0.3–0.5 mm wide (Fig. 156). Just below the inflorescence the culm is angular, scaberulous on the angles, rarely also on the faces. The leaves are all basal and form tufts. The leaf sheath is 5–7 mm long; on the laminar side of the sheath (the side which bears the blade) the visible longitudinal nerves are close together; the contralaminar side of the sheath is membranous and thin-textured. The leaf blade is 5–7 cm long and 0.7–1.0 mm wide at the base, narrowly linear, gradually narrowing to the apex, the ventral surface concave, margins and midvein (sometimes also the lateral veins) scaberulous. The lowest bract of the inflorescence is leaflike, up to 1.5 cm long.

The inflorescence is a delicate anthela of 3–7 rays 1–8 cm long (Fig. 157). Each ray is a sympodial axis. The rays arise at the tip of the peduncle separated by very short internodes. Each ray is subtended by a bract. The base of the ray is swollen and surrounded by a tubular prophyll. The prophyll is 3.5 mm long with an oblique mouth and has two short pointed extensions on the adaxial side of the apex (sometimes these appear to be on the abaxial side due to torsion).

The rays bear pseudospikelets, very tiny vegetative shoots, and groups made up of both of these structures. (Details are given below.)

The pseudospikelet is fusiform and elliptical, 2.8–3.5 mm long and 0.45 mm wide; it has a short pedicel. The number of glumiform bracts in a pseudospikelet is 3–4 (rarely 5) (Figs. 158–161, 163–164). The first or lower glumiform bract is always empty; the second is never empty but covers a pseudanthium (a structure that looks like a bisexual flower but in this species is made up of a short axis or rachilla, bearing laterally two male flowers of one stamen each and an apparently terminal female flower of a single pistil). The third glumiform bract usually covers a pseudanthium but sometimes is empty. The fourth and fifth glumiform bracts when present are always empty. The pseudospikelets that terminate a ray (rarely one along a ray) are generally associated with a tiny vegetative shoot which arises in the axil of the glumiform bract that is immediately below the basal bract of the pseudospikelet.

Staatsherbar. München

FIGURE 156. Holotype sheet of *Micropapyrus viviparoides* Süss.; *Luetzelburg 22381*; × 0.4. Figures 157–164 are from plants of this sheet.

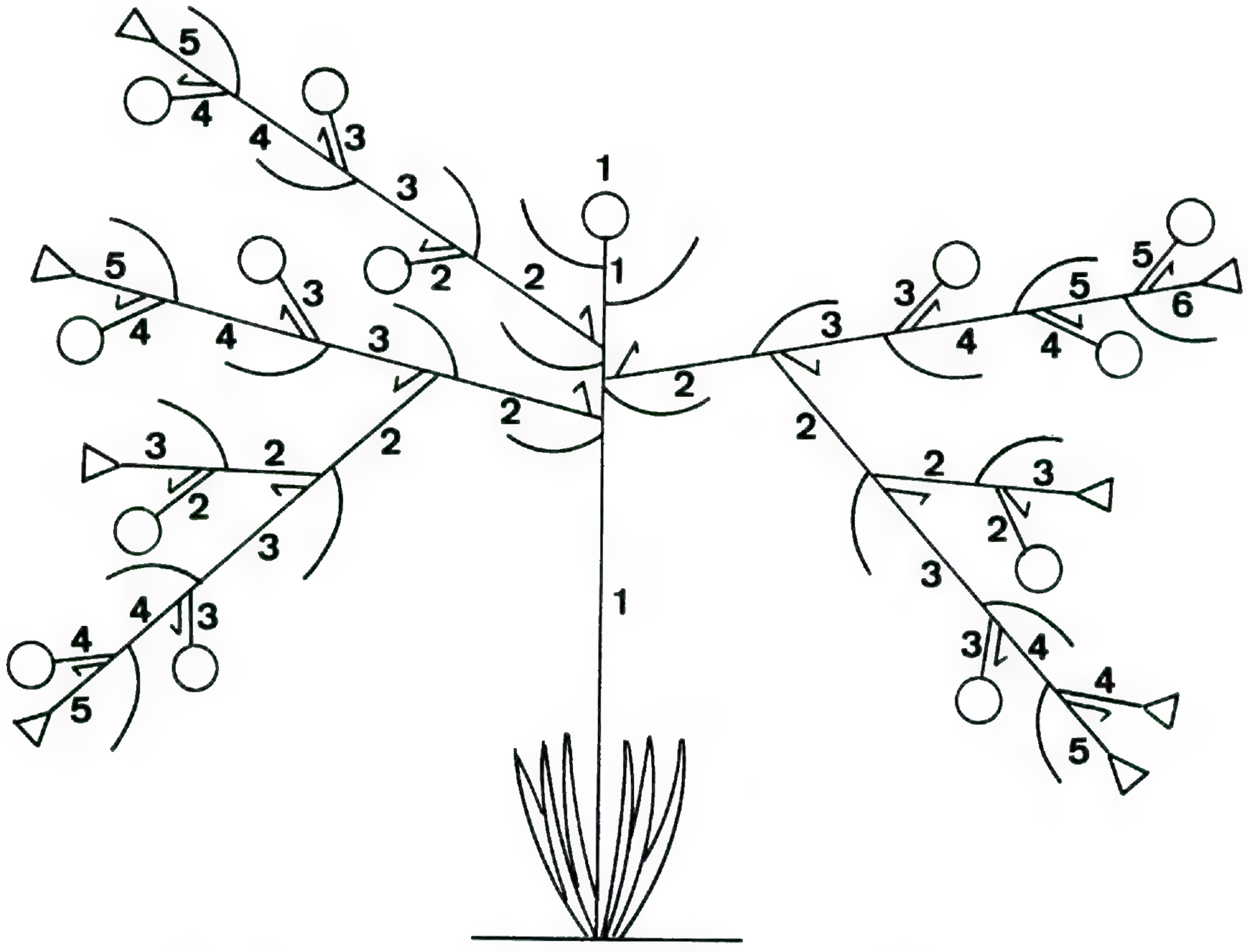


FIGURE 157. Branching pattern of an actual plant examined. The branching orders are represented by numbers. The curved lines represent bracts, the short hooked lines the prophylls. Circles indicate pseudospikelets and triangles vegetative shoots. Axis no. 1 is the culm (peduncle) from whose apex the rays of the inflorescence arise and which continues on to form the axis of the terminal pseudospikelet. This axis is monopodial. The rays and subrays are sympodial, that is, formed of the first two basal internodes of successively higher-order branches. (For reasons of clarity, a newly arisen axis is shown slightly separated from the bract in whose axil it arises. This slight separation is of course not to be considered an internode. The slight separation along an axis from its origin to its prophyll is, however, a genuine internode (the subprophyllar internode).)

The pseudanthia do not emerge from the pseudospikelet axis (rachis) at the nodes, that is, in the axils of the glumiform bracts. They emerge, that is, physically separate from the axis, in the middle or upper part of the internode. However, morphologically, the pseudanthium axis (rachilla) has its origin at the same node as the glumiform bract immediately below it; its axis grows adnate or concrescent to the pseudospikelet rachis (phenomenon of "concaulescence," Troll, 1964: 127–129), and only separates above (Figs. 160, 163–164).

In the pseudanthium, the female flower is always apparently terminal on a stipe 0.2–0.4 mm long. It consists of a single pistil with two stigmatic branches and is surrounded at the base by three smooth sinuous bristles. The stipe has two male flowers which arise at different levels (Figs. 160–164).

The fruit is ovoid-apiculate, short-stipitate, 1.6–2.0 mm long (including the apical point and the stipe) and 0.35–0.6 mm wide (Figs. 160–161).

The branching pattern of the whole inflorescence of this plant merits a full

presentation (Fig. 157). The peduncle (culm) does not bear cauline leaves; it acts as the lowest internode of the first-order axis of the inflorescence. At its tip arise the several rays of the inflorescence, 3–7 in the plants examined. Each ray arises at a node and is separated from the node of the next ray by a very short internode. Since there are 3–7 rays, the number of internodes is 2–6. Immediately above the uppermost ray is a pseudospikelet, or this is separated from the uppermost ray by 1–2 nodes with glumiform bracts. Thus 1–3 internodes intervene between the node of the uppermost ray and the node where the lowermost bract of the pseudospikelet arises. The pseudospikelet on the tip of the peduncle has 3 (very rarely 4) internodes, one between each two consecutive bracts.

Each ray which directly arises from the peduncle has as its basal internode the first internode of a second-order axis (branch of the peduncle). This first internode is very short and ends at the node bearing the prophyll of the second-order branch, that is, it is a subprophyllar internode. The branch continues with a second internode which because it is longer and visible appears to be the first or basal internode of the ray. The ray continues with its third internode being the first internode of a third-order axis. This is also short and terminates at a node with a prophyll. This third-order branch then continues with a longer visible internode that appears to be the second internode of the ray although it is really the fourth, etc. Thus, the ray is made up of a single line of the first two internodes of branches of successively higher order. Each short internode of the ray (i.e., the beginning of each new branch) is subtended by a bract and ends at a node with a prophyll. In other words, the growth of the ray is sympodial.

The lower rays emit subrays. At the node in which the basal long internode of a lower ray terminates, the second order axis turns aside, forming the basal internode of the subray. The upper rays do not emit subrays. Here the second-order axis terminates directly in a "lateral group." The last internode of a ray or subray ends in a "terminal group."

The expressions "lateral group" and "terminal group" are applied to the pseudospikelets and miniscule shoots which, together or alone, form the groups of organs that can be seen along the rays and subrays (Figs. 158–160). Among those examined, I found the lateral groups almost always composed of a single pseudospikelet (Figs. 158, 160), but sometimes it was composed of a pseudospikelet and an associated shoot (Fig. 159).

The terminal groups are usually composed of a pseudospikelet plus an associated shoot; very rarely the terminal group was made up of two shoots without a pseudospikelet.

In general, the second internode (first long internode) of an axis of branch order n forms the $(n\text{-}1)$th long internode of a ray or subray. The distal internodes of a branch form the axis of lateral or terminal groups. When a group is made up of a pseudospikelet and a shoot together, the axis of the shoot is a side branch that arises at the base of the pseudospikelet.

In one case examined a terminal group was made up of two shoots without a pseudospikelet. The axis of this group was of the fourth order; its continuation

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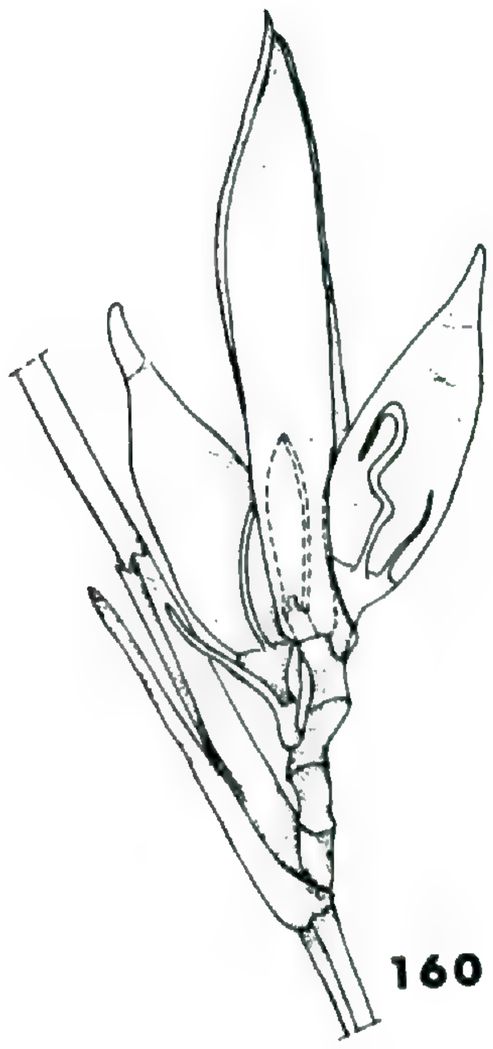

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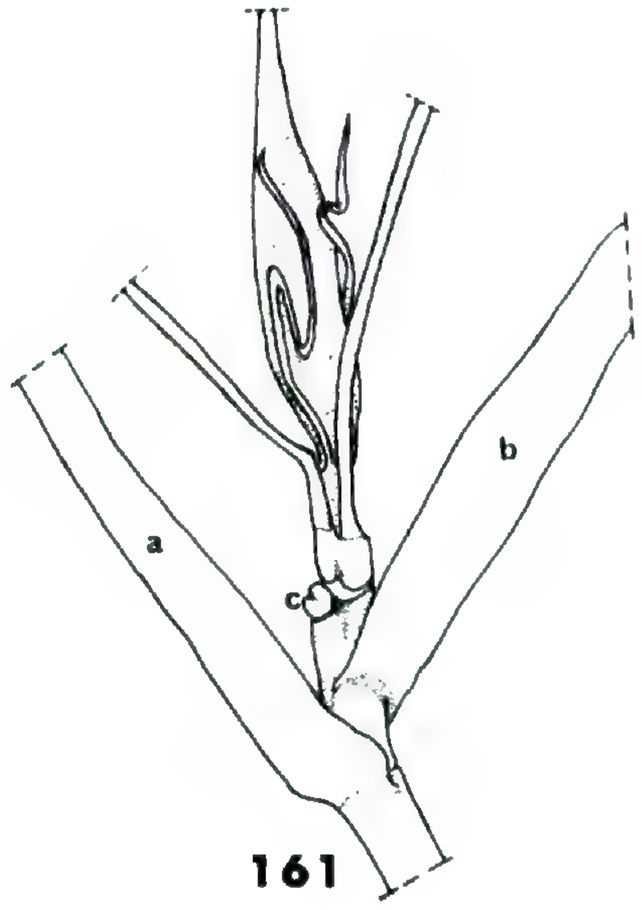

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FIGURES 158–161.—158. Part of a ray with a "lateral group"; × 8. The lateral group is here made up of a pseudospikelet (right) whose axis is the termination of the stem coming from below. Bract a, also on this stem, subtends a new branch whose first two basal internodes (a short one and a long one) continue the ray and which bears a prophyll, b, at the node which separates these two internodes.—159. Part of ray with a "lateral group"; × 8. This lateral group is made up of a pseudospikelet and a vegetative shoot. The stem from below continues on to form the axis of the pseudospikelet. Below the pseudospikelet is a bract, a, on the same axis. From its axil arises a new branch which forms the axis of the vegetative shoot. The first lateral organ on this new branch is a prophyll, b, which is part of the shoot. Further down the original stem is bract c, from whose axil arises a second new branch, d, which bears a prophyll, e, and which continues the ray.—160. Part of ray showing a "lateral group" formed of a pseudospikelet; × 14. The first, second, and third glumiform bracts have been removed, exposing the first four internodes of the axis of the pseudospikelet (rachis). The stipe of the fruit (rachilla of the true spikelet which forms the pseudanthium) to the left originates at the second node of the rachis but emerges in the middle of the third internode; the stipe of the fruit to the right originates at the third node but emerges near the top of the fourth internode. Both are cases of concaulescence. The fourth glumiform bract, shown at the top of the rachis, encloses a fifth bract (shown in dashed outline) which covers the tip of the rachis.—161. Pseudospikelet with basal glumiform bracts a and b spread apart, showing its one pseudanthium in fruit; × 33. The third glumiform bract was removed on the left side, leaving its scar and exposing a small bilobed projection, c, which is the apex of the rachis of the pseudospikelet. It appears lateral because of the development of the pseudanthium, which appears terminal. This pseudanthium really originates in the axil of the second bract, b, but remains concaulescent to

FIGURES 162–164.—162. Young pseudanthium of two male flowers of one stamen each, and female flower of a single pistil. At this stage one does not always find bristles, so that the pseudanthium looks even more like a true flower; × 29.—163. Pseudospikelet with its four glumiform bracts removed, showing the rachis; × 29. The tip of the rachis, a, is at the base of the rachilla of the pseudanthium.—164. Semidiagrammatic representation of a pseudospikelet with three glumiform bracts and two lateral pseudanthia. The first bract is empty. The rachilla of the lower pseudanthium originates in the axil of the second bract but emerges from the rachis only in the middle of the internode. The rachilla of the upper pseudanthium originates in the axil of the third (uppermost) bract but emerges at the extremity of the internode, appearing terminal. This rachilla appears to be a further extension of the pseudospikelet rachis, although it is really a new axis lateral to it. The base of the rachillas thus show concaulesceuce with the rachis.

formed the axis of the first shoot, and its only branch (a fifth-order axis) formed the axis of the second shoot.

Süssenguth described the pseudanthium ("Scheinblüte") as made up of a female terminal flower and a masculine flower of two stamens. Schultze-Motel (1959), in his discussion of *Micropapyrus*, repeats Süssenguth's description and

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the rachis internode and only emerges at the upper end of this internode near the rachis tip. The rachilla of the pseudanthium (with two filaments arising at different levels on it) appears to be a continuation of the pseudospikelet rachis but is really a new branch lateral to it. Two sinuous bristles arise at the base of the fruit.

illustration without disagreeing on the number of flowers in the pseudanthium or the number of stamens in the male flower. But, from the position of the stamens at different levels on the rachilla it is clear that each stamen is a separate male monandric flower. No undoubted pseudanthia are known in the Cyperaceae in which the male flowers have more than one stamen.

Süssenguth (1943) interpreted the hypogynous bristles as perianth or "intrastaminale Diskusorgane." Like Schultze-Motel (1959), I interpret the hypogynous bristles to be transformed bracts, that is, glumellas which have taken on the form of bristles.

I agree with Süssenguth that *Micropapyrus* is an independent genus. The structure of the inflorescence and type of pseudanthium justify its establishment. However, I disagree with his view that there is a relationship between *Micropapyrus* and the Rhynchosporeae. The latter have true spikelets and true flowers while *Micropapyrus* has pseudospikelets and pseudanthia. These structures are so different from those of the Mapanieae, however, as well as different from those of *Syntrinema*, that *Micropapyrus* should be placed in a new separate tribe, Micropapyreae.

Micropapyreae differ from the Mapanieae in the following characteristics:

1. The general habit of the plant and inflorescence are different.
2. The pseudospikelet consists of only 3–4(–5) large covering bracts with 1–2 pseudanthia instead of the dozens or hundreds of small covering bracts and pseudanthia of a pseudospikelet of the Mapanieae (expect for *Chrysithrix*).
3. The only glumellas present, the three at the base of the pistil, are in the form of bristles and not laminas as in all the Mapanieae.
4. The usual two lower, lateral, folded, ciliate-keeled glumellas of the Mapanieae are lacking.

Micropapyreae differ from the Syntrinemeae in the following characteristics:

1. The general habit of the plant and inflorescence are different.
2. The pseudospikelets are visibly separate bodies and not densely clustered in a head as in the Syntrinemeae.
3. The pseudospikelets are all bisexual instead of bisexual and male as in the Syntrinemeae.

Other differences between *Micropapyrus* and *Syntrinema* are more at the level of genus than of tribe, such as, in *Micropapyrus*, the presence of tiny vegetative shoots on the inflorescence branches, the lack of a subtending bristle with each male flower (stamen), the presence of two male flowers instead of three, and the sinuous, glabrous, hypogynous bristles rather than the straight, shortly hairy bristles of *Syntrinema*. In fact, the only similarity in the two genera is that both have relatively few pseudanthia per pseudospikelet and both have three hypogynous bristles in the bisexual pseudanthia.[3]

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[3] Since writing the above, I have seen two more collections of this species from Brazil, the first since the type; they were sent to me from Amazonia. These are: Pará, Rio Univini, Igarapé do Campo, 25 Apr. 1974, *Pires et al. 14257*. Pará, Rio Xerinini (Projeto RADAM, Ponto 07A, Quadrícula SA-20-X-A), *Pires et al. 13932*.

The plants of these two collections appear identical in habit to those of the type and have the same sympodial branching of the inflorescence rays. Like the type, the rays bear pseudo-

Micropapyreae L. T. Eiten, trib. nov. Pseudospiculae separatae dispersae secus ramos inflorescentiae; pseudospicula 3–4(–5) bracteis tegentibus et 1–2 pseudanthiis bisexualibus; quidque pseudanthium 2 floribus masculinis unistaminatis (sine glumellis subtentis) et 1 flore femineo unipistilato terminali (pseudoterminali?) cum 3 glumellis setiformibus hypogynis.

Type genus: *Micropapyrus* Süss., Bot. Jahrb. Syst. 73: 115–116. 1943.

Websteria submersa (C. Wright) Britton

(included in *W. confervoides* (Poiret) Hooper)

Description based on the following types: isotype fragment of *Scirpus submersus* C. Wright in Sauvalle, Fl. Cubana, 175–176. 1868: Cuba, *Wright 3775* (M); holotype and isotypes of *Websteria submersa* var. *negrensis* Süss., Bot. Jahrb. Syst. 73: 124–125. 1943: Brasil, Amazonas, Barra do Rio Negro, Oct.–Nov. 1819, *Martius 2810* (M); holotype and isotypes of *Websteria submersa* var. *leutzelburgii* Süss., Bot. Jahrb. Syst. 73: 125. 1943: Nordbrasilien [Território de Roraima], Paren-intôe, Serra do Sol, igarapé, in einem 3 m tiefen Wasserloch des Falls, Oct. 1927, *Luetzelburg s.n.* (M).

The plant grows submersed, carpeting lake bottoms, with roots fixed to the substrate and the culms buoyed up in the water or the upper part of the plant floating near the surface. It forms long thick stems from which whorls of culms arise at intervals (Figs. 166–168, 188–189). The culms are capillary, cylindric-sulcate or trigonous, slightly flattened and smooth. Many of the culms in a whorl branch at their tips forming new apical whorls; 4–19 culms per whorl were noted in the collections examined. The culms in the more distal whorls are progressively thinner, the last being 0.1–0.3 mm wide (Figs. 165, 170, 190). In some plants of other collections there are no long thick stems which give off whorls; instead a rooted whorl arises directly from the substrate, as a clump, and culms of this basal whorl have whorls at their tips, etc. (The "whorls" here referred to are shoots with the branching pattern shown in Fig. 110.)

The internodes between successive whorls are usually progressively shorter distally, except for the culms of the last whorl which may be very much longer than the internodes immediately below them (Figs. 165, 170, 190). Among the culms that make up a whorl, some form new whorls at their tips while others do not branch. The culms that have spikelets at their tips (peduncles) are longer, of equal length, or shorter than the other culms of the same whorl and are definitely thicker (Figs. 171, 190). The culms that arise from the whorl node (a compound node made up of a close succession of true nodes, one for each culm)

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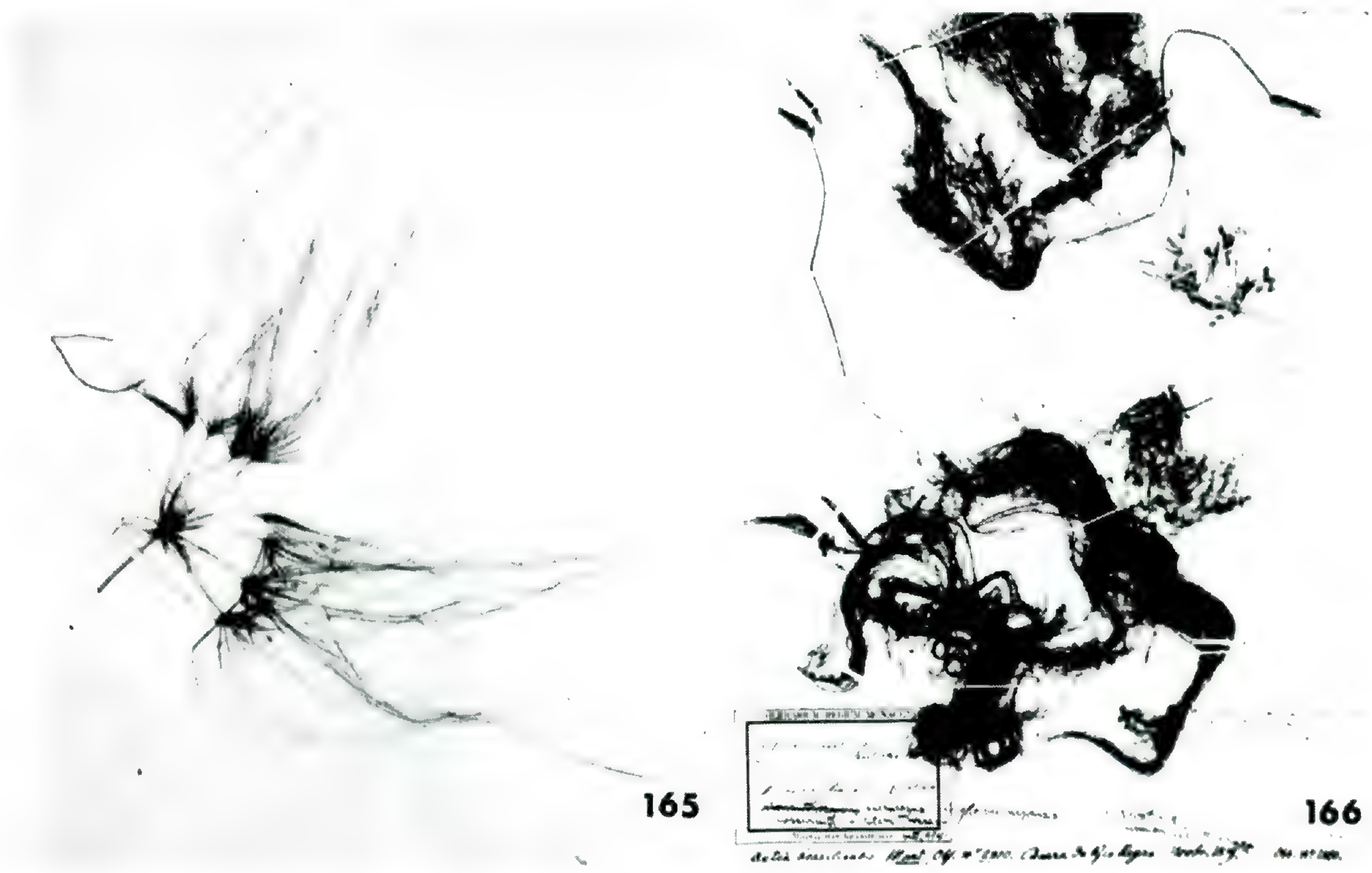
spikelets and miniscule shoots although in some of the inflorescences the latter are less frequent than in the type. The two new collections also have 1–2 pseudanthia in each pseudospikelet. The pseudospikelets are 3.0–3.5 mm long; the fruits are 1.5–1.8 mm long by 0.4–0.6 mm wide, with a dark honey-colored body and blackish brown apical point. The concaulescence of the stipe of the pseudanthium is such that it is embraced by the glume next above the one from whose axil it really arises. The hypogynous bristles are shorter, thinner, and straighter than those in the type collection. The level at which the stamens arise on the pseudanthium axis below the fruit is closer to the fruit base than in the type so that the conjunction of stamens and fruit make the pseudanthium appear even more like a true flower.



Figures 165–166.—165. Fragment of isotype of *Scirpus submersus* C. Wright, basionym of *Websteria submersa* (C. Wright) Britton; *C. Wright 3775*; × 0.2.—166. Lectotype of *Websteria submersa* var. *negrensis* Süss.; *Martius 2810*; × 0.2. Figures 170–187 were made from plants of this collection.

do not always develop simultaneously. Thus, in the same whorl with older culms may be found young culms still within their long, narrow hoodlike leaf sheaths.

Two scalelike bracts are found outside of and below each whorl (Figs. 169, 171, 191–193); the lower subtends the oldest culm in the whorl. It is triangular or elliptical, obscurely 3-nerved, 6.5–11.0 mm long and 0.6–1.6 mm wide in the lower whorls of a plant, and 0.75–2.0 mm long and 0.3–1.0 mm wide in the terminal whorls. This lower external bract has a median longitudinal thick portion streaked with reddish brown lines, an apiculate or blunt apex, and membranous sides whose margins in the material seen were partially or totally decayed. The upper external bract, although apparently "below" the whorl, is really distal to it on the culm whose tip bears the whorl. (This is also true in *Eleocharis* culm tip shoots; see Figs. 109 F, bract e; 110, bract b.) The upper bract is also triangular or elliptic with rounded apex; in the lower whorls it is 0.4–5.2 mm long and 1.6–2.0 mm wide, and in the terminal whorls it is 0.5–1.7 mm long and 0.2–0.8 mm wide. This bract does not have visible nerves; it is thinly membranous, hyaline and falls to pieces easily.

Within a whorl, between the culm bases, there are short or long triangular laminas with two convergent veins and an acute or obtuse apex (difficult to make out in Figs. 169 and 171; very visible in Fig. 191). These laminas are very thin and fall to pieces easily. It seems as if each lamina is associated with a culm, but due to ease of its decomposition in the water, there is almost never a correspondence between the number of laminas and culms. It is not possible to de-

FIGURES 167–168. Isolectotypes of *Websteria submersa* var. *negrensis* Süss.; *Martius 2810*; × 0.2. Figures 170–187 were made from plants of this collection.

cide from the plants themselves if these laminas are bracts subtending the culms or if they are prophylls and therefore on the same axis as the culms. They do not have the typical form of prophylls, that is, they have acute, not retuse apices; however, they do have the double venation characteristic of prophylls. Their exact position cannot be verified because the internodes between the culms making up a whorl are extremely short. However, since I believe *Websteria* evolved directly from *Eleocharis* and since in that genus the culm axes have basal prophylls, the similar laminas in *Websteria* are probably also of this organ.

The base of each culm is enclosed in two leaf sheaths (Figs. 169, 171, 191). The lower (outer) sheath is tubular, short, membranous, light-colored or tinged with reddish brown, and it has an oblique mouth; the upper (inner) sheath is long-tubular, membranous, light-colored or greenish, streaked with reddish brown lines, and it has an oblique mouth.

The apices of those culms that do not bear whorls or spikelets at their tips are bare and smooth; the tips are not covered by scalelike bracts as in *Eleocharis* (Fig. 203).

The peduncles bearing spikelets arise among the culms that form the antepenultimate and penultimate whorls. They are 2.3–5.1 cm long and 0.35–0.9 mm wide. They have two leaf sheaths; the lower decomposes easily. Sometimes it splits longitudinally on one side and so forms a lamina that may be confused with the basal lamina of the peduncle (prophyll), or it may become fragmented and

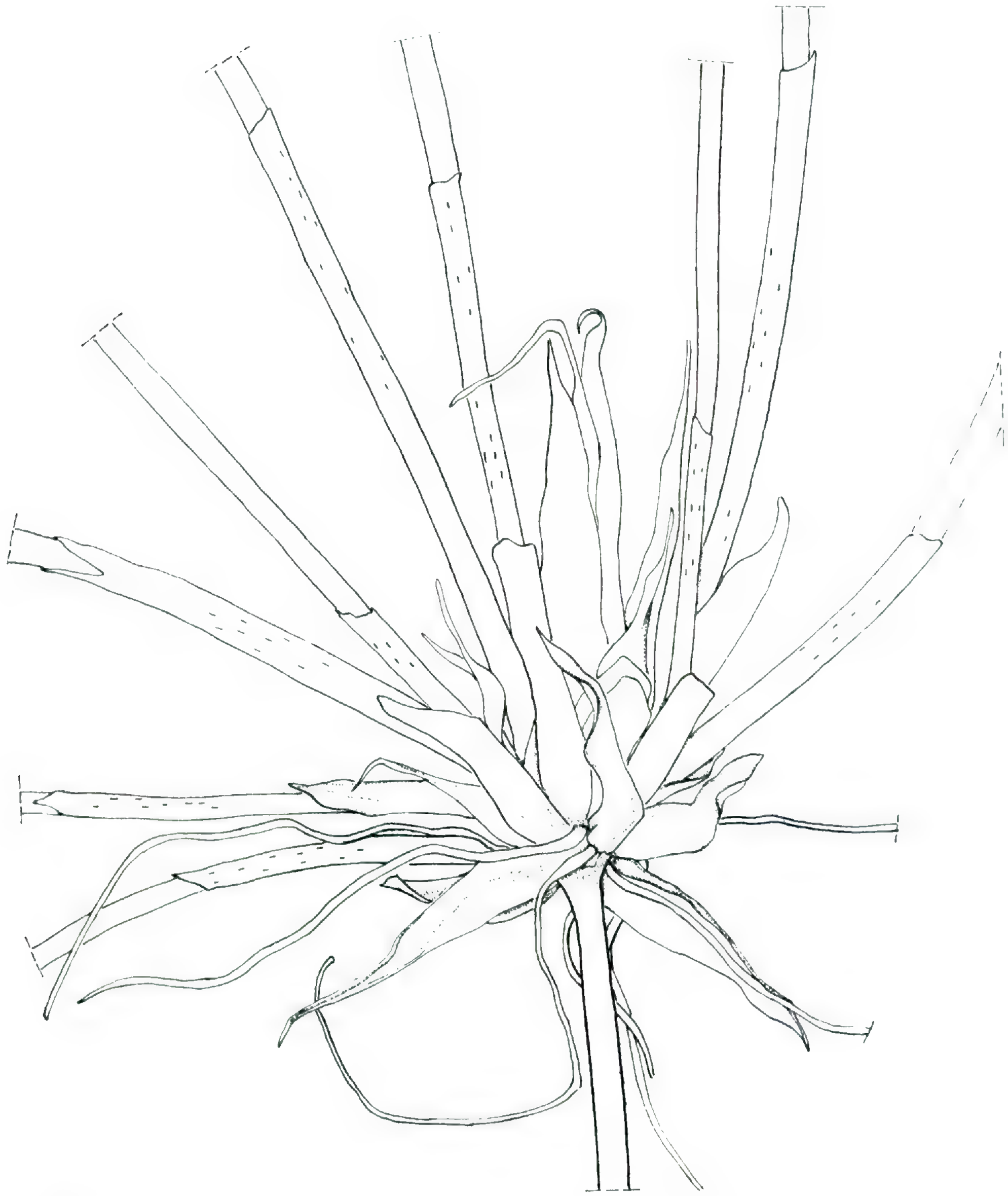
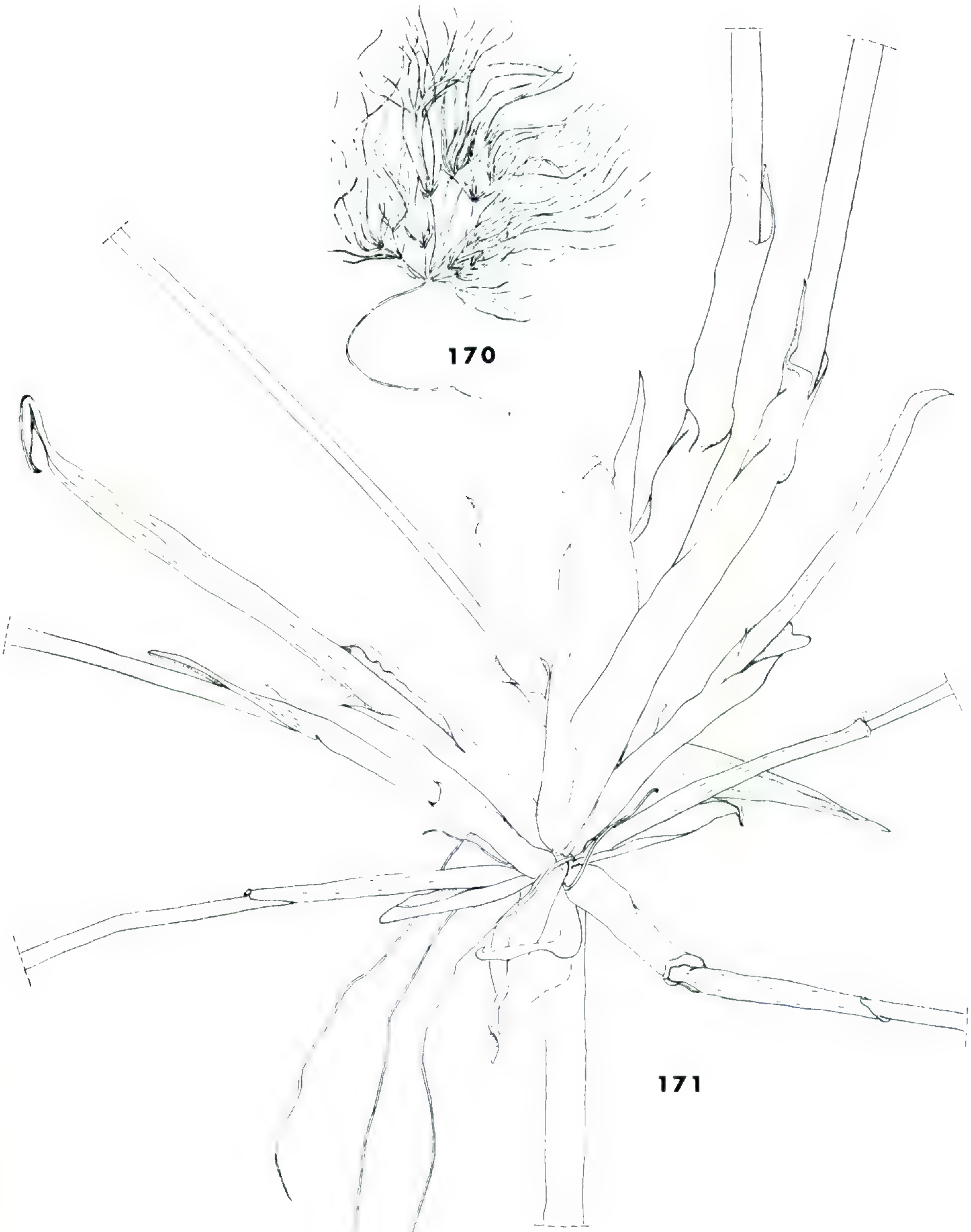
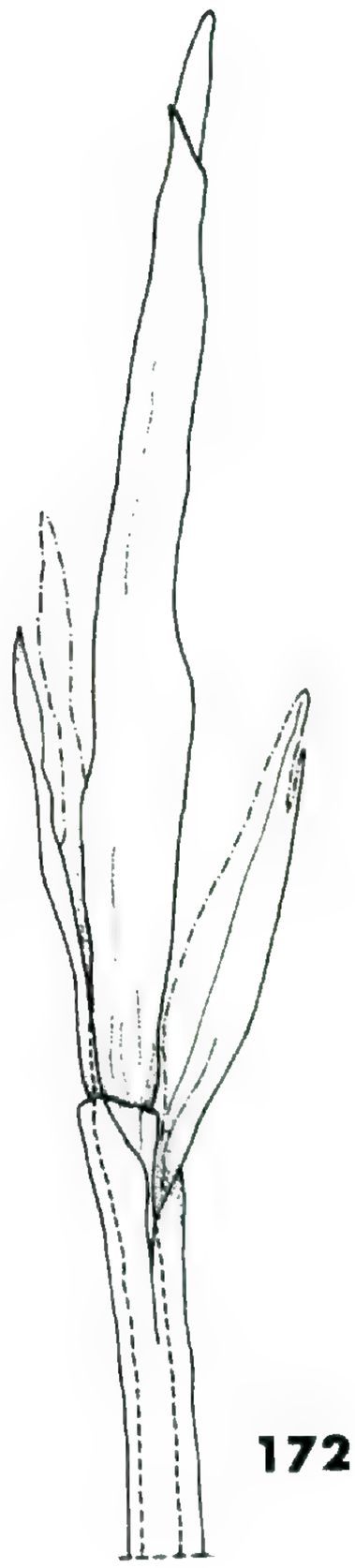


FIGURE 169. Detail of base of penultimate whorl; *C. Wright 3775*; × 16. Note from below to above, upper part of culm which bears the whorl, seven adventitious roots from culm bases, the two external bracts at the base of the whorl, base of nine developed culms with their two leaf sheaths (the upper streaked with short lines, the lower split open in some cases), and in the center several young culms still covered by their leaf sheaths. The prophylls were not seen and probably had rotted away.

disappear. The upper sheath covers the peduncle and its apex frequently covers the base of the spikelet (Figs. 172–173). This sheath is membranous and loose; its mouth is torn by the developing spikelet or decays or splits on one side, so that the apex of the sheath appears like a lanceolate leaf blade (Figs. 174–175).



FIGURES 170–171.—170. Branching of part of plant; × 0.4.—171. Detail of base of whorl; × 12. Note from below to above, tip of culm which bears the whorl, adventitious roots from culm bases, the two external bracts at the base of the whorl (one in front, the other behind the whorl at right), base of five developed culms and three young culms (the upper leaf sheath streaked with short lines, the lower sheath split open in some cases), and two thick peduncles with sheaths. The prophylls were not seen here and probably had rotted away.



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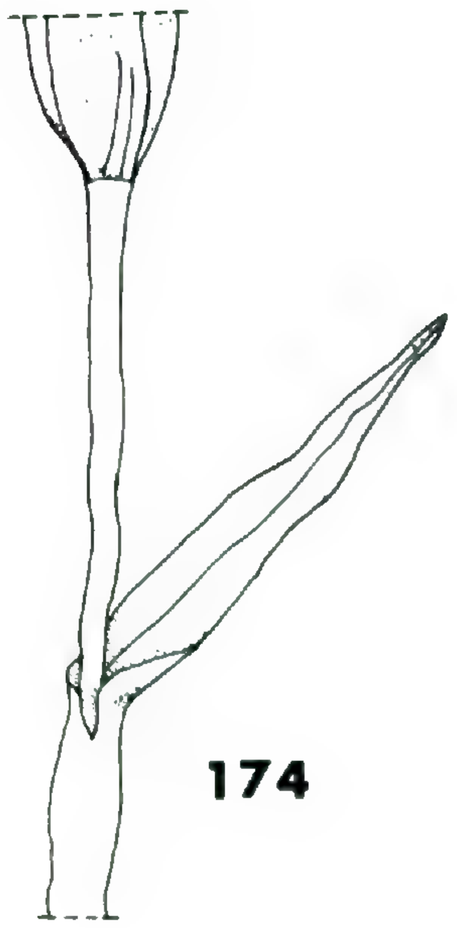

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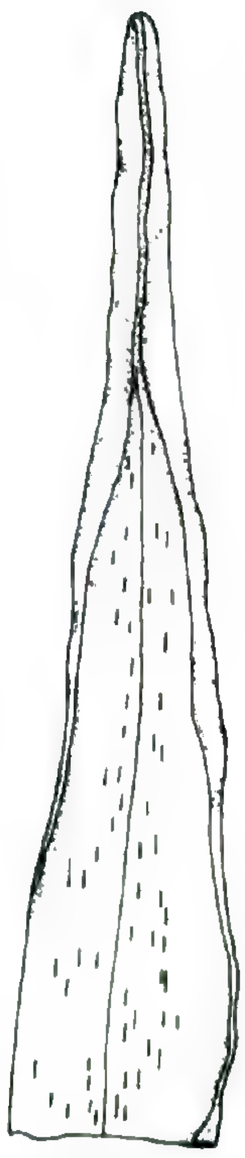

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Each peduncle bears one terminal spikelet (Figs. 176, 194, 199). The spikelets are long, elliptic or long-ovate, 9–11.7 mm long and 0.7–1.25 mm wide. Each spikelet always has a true glume (Figs. 178–179, 195) and a single flower; just below the spikelet and looking like it is part of an associated scale (Figs. 177, 180, 196, 198). The associated scale envelops the glume and has been counted in the dimensions of the spikelet as given above.

The associated scale is always empty. When still young, it forms a flattened tube with a vertical fold along the side opposite to its dorsal median portion (Fig. 183). The median portion is thicker and streaked with reddish brown lines. The inner true glume is membranous; when young, it is enrolled (Fig. 197) or it is tubular with a similar longitudinal fold which faces the dorsal part of the outer associated scale (Fig. 183). The true glume surrounds a bisexual flower. During development of the ovary, the tubular associated scale and glume split along the vertical folds whose tissue is initially thinner, and both laminas assume the typical form of glumes (Figs. 177–178, 184, 195–196).

The flower has three stamens with long-oblong anthers and a pistil with an ovoid-trigonous ovary and a long style with two long, pilose stigmatic branches (Figs. 179, 181, 200). Flowers may contain bristles (Figs. 181–182, 184, 200–201) or when young may still lack them (Figs. 179, 183).

The body of the achene is pyriform, 2.0–3.5 mm long and 1.5–2.1 mm wide. It has a subulate mucro 1.5–2.4 mm long with a vertical depression at its base reaching halfway up the mucro (Fig. 187). In other achenes (which perhaps are immature) the transition from body to mucro is wrinkled, at least when dry (Fig. 185). The surface of the achene is finely tuberculate with a hexagonal or pentagonal reticule (Fig. 186). There are 7–14 retrorsely spinulose bristles arranged in two series (Figs. 185, 187).

The material at present called *Websteria submersa* was originally described by Charles Wright (1868) as *Scirpus submersus*, based on *Wright 3775*, from lakes in Pinar del Río. It is sometimes still called by this name (Barros, 1960). Charles Wright described his plant as having 1-flowered spikes with two glumes; in anthesis the spikes were scarcely emersed and thereafter submersed. He considered the thick stems as stems and the thin stems as leaves. He mentioned 8–

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FIGURES 172–180.—172. Upper part of peduncle (in dashed outline) with spikelet; × 6.4. The upper part of the upper leaf sheath is here torn into three parts partially surrounding the spikelet.—173. Base of spikelet in fruit, showing separation of borders of associated scale and the very oblique mouth of upper leaf sheath; × 6.4.—174. Peduncle and base of spikelet; × 6.4. Mouth of upper leaf sheath has decayed on one side, leaving other side appearing like a leaf blade.—175. Diagram showing how this arises. Shaded area of apex of upper leaf sheath represents part which decays; the rest remains to form the pseudoblade.—176. Peduncle tip and spikelet with its enrolled associated scale and glume in natural position; × 6.4.—177. Associated scale spread out, showing adaxial side streaked with short lines; × 6.4.—178. Glume spread out, showing adaxial side; × 6.4. The upper margins are short-ciliate and are shown here slightly enrolled.—179. Spikelet with associated scale removed and glume cut open to show young flower; × 6.4. The pistil has a very small narrow ovary and two pilose stigmatic branches. There are three stamens. Note absence of bristles in this young-flower stage.—180. Associated scale spread out, showing adaxial face and three parallel veins convergent at apex; × 6.4.

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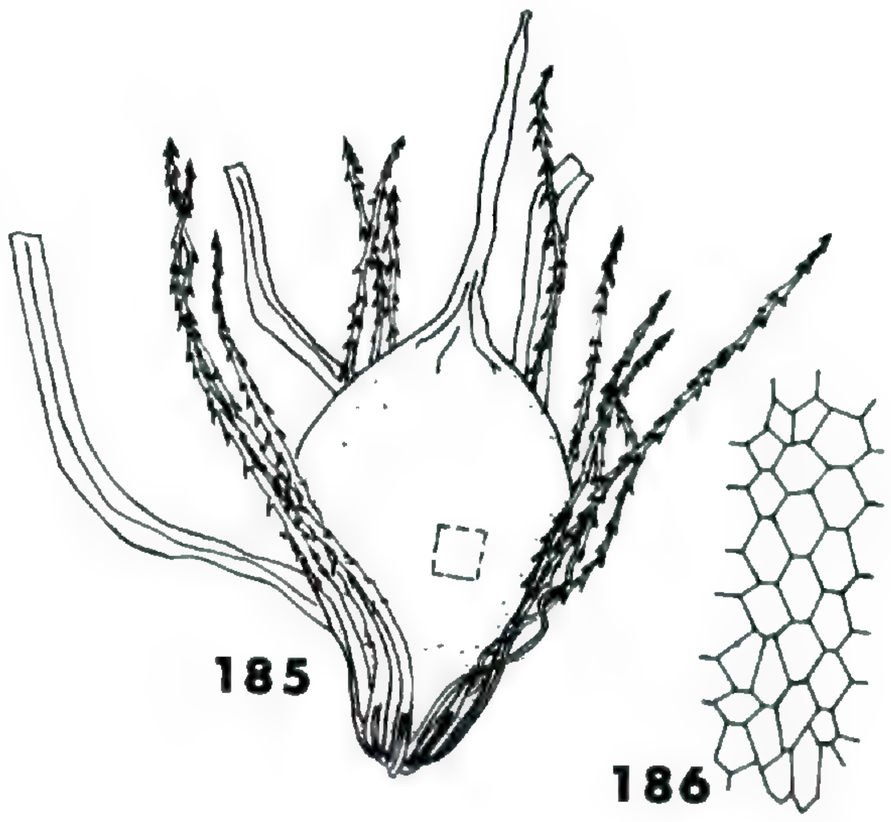
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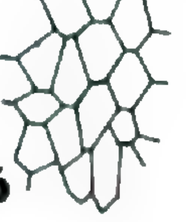
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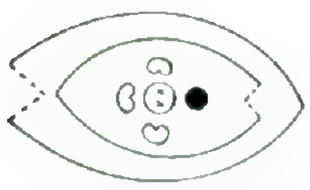
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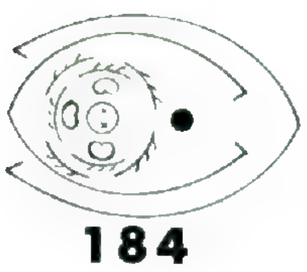
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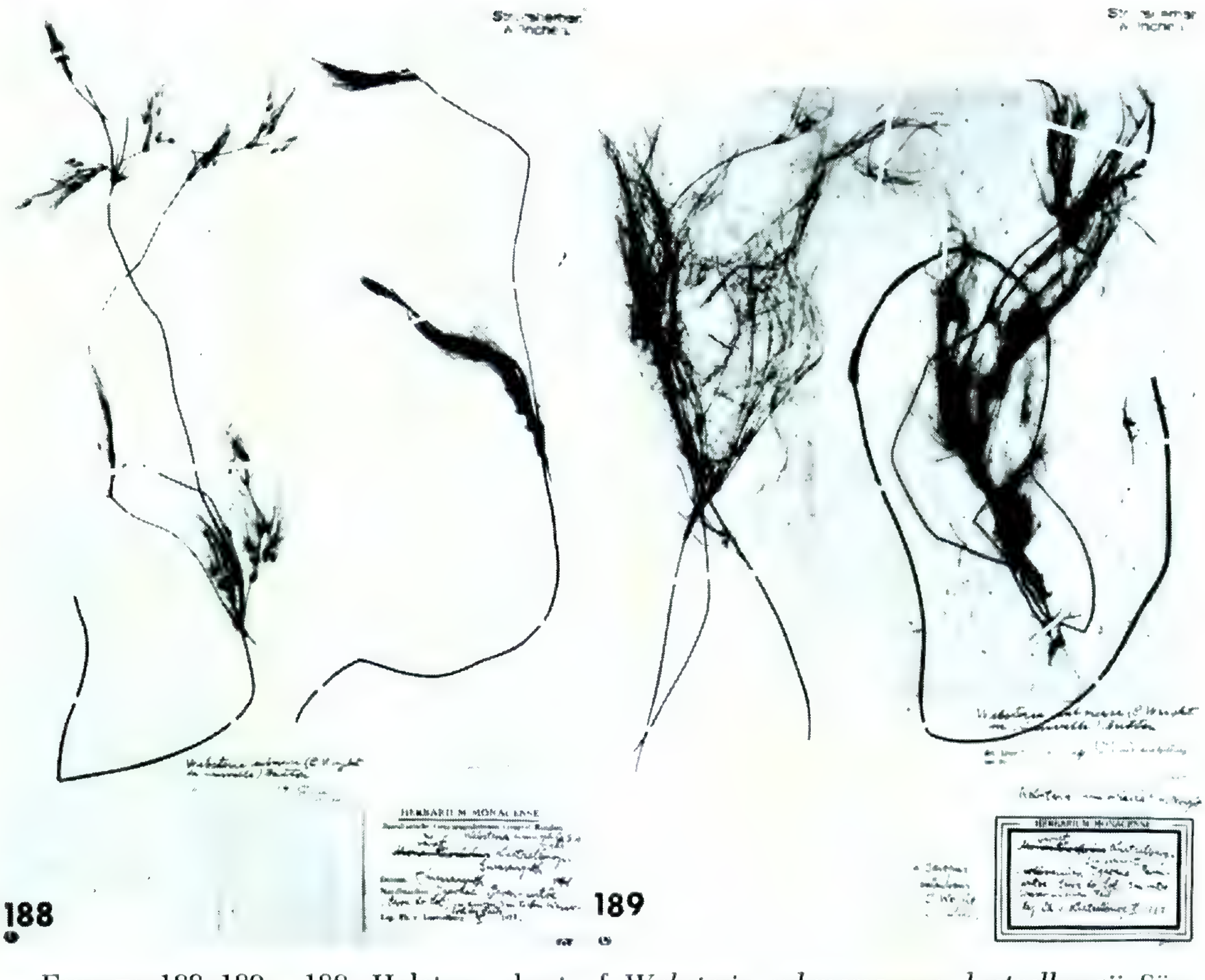
FIGURES 181–187.—181. Spikelet in mature flower with associated scale removed and glume spread out; × 6.1. Note pistil with thin ovary, three filaments (only bases shown), and ten bristles.—182. Detail of a bristle showing retrorse hairs; × 25.—183. Floral diagram of a young spikelet with the associated scale and glume still closed, forming tubes. Dashed line shows fine tissue along which these tubes will later split. Note absence of bristles. The dark point represents the apex of the rachilla and its position is meant to show that the flower is really lateral (pseudoterminal).—184. Floral diagram of a mature spikelet with open associated scale and open glume and two series of bristles.—185. Mature achene with filament bases and bristles; × 9.2.—186. Detail of reticulated surface of achene in square area in Fig. 185; × 25.—187. Mature achene with bristles and filaments; × 6.2.

10 bristles for the achene. Samuel Hart Wright (1887) described a new genus, *Websteria*, with one species, *W. limnophila*, based on several collections: *S. H. Wright s.n.*, December 1886, and *G. W. Webster s.n.*, April–May 1886, both from lakes in Volusia County, Florida, U. S. A. Britton (1888) noted that the type of *Scirpus submersus* and those of *Websteria limnophila* belonged to the same species. Britton agreed with S. H. Wright that this species constituted an independent genus and therefore designated it *Websteria submersa* (C. Wright) Britton because *submersus* was the oldest epithet of those treated.



FIGURES 188–189.—188. Holotype sheet of *Websteria submersa* var. *luetzelburgii* Süss.; *Luetzelburg s.n.*, Oct. 1927; × 0.2. Figures 191–201 were made from plants of this collection. —189. Isotype sheet of *Websteria submersa* var. *luetzelburgii* Süss.; × 0.2.

After having seen the types of *Scirpus submersus*, *Websteria submersa* var. *negrensis*, *W. submersa* var. *luetzelburgii*, and one of the syntypes of *W. limnophila*, I concluded they all belonged to the same species. Because of its distinctive branching and habit and distinctive large 1-flowered spikelets, I agree that *Websteria* is an independent genus. It is neither a *Scirpus*, nor as Hooper (1973) reduced it, a species of *Eleocharis*.

I do not believe the two varieties erected by Süssenguth can be justified. The material of this species that was examined shows little variation between collections and such as there is can be expected in aquatic plants. No collection has characters so marked as to justify the erection of a variety. For this reason I have given a description based on the three types together.

It is now necessary to enter into a discussion of some Old World plants which apparently are part of the *Websteria* complex and to consider their relation to the New World plants. Poiret (1804: 755) published *Scirpus confervoides* from a specimen of Petit-Thouars from pools of water in Madagascar. Poiret thought the plant had a certain relation to *Scirpus fluitans* L. and apparently for this reason placed it in *Scirpus*. It had long stems with verticillate fascicles of elongated "leaves" finer than a hair. From the center of the fascicle arose 1–several filiform culms each with a basal sheath which was slightly lanceolate at its apex.

Figure 190. Isotype fragment of *Websteria submersa* var. *luetzelburgii* Süss.; × 0.85. It shows whorled, thin culms and thicker peduncles with spikelets.

Each culm terminated in a solitary oval "spike" composed of a few inner whitish membranous scales enveloped by two external subulate acute long scales. The description (there was no illustration) thus could be the same as *Websteria submersus* except for the extra inner glumes in the spikelet.

Various authors in the ensuing decades listed the name *Scirpus confervoides* but not all seemed to be referring to the same species. Kunth (1837: 173) described a specimen in the Willdenow herbarium, no. *1123* from Madagascar, under this name. (Willdenow had labelled it as *Schoenus confervoides*.) Kunth mentions crowded, fasciculate, long capillary "leaves" and large, linear, 1-flowered "spikes" with two glumes which are oblong, obtuse, trinerved, glabrous, the outer surrounding the inner. This could be a *Websteria*. Boeckeler (1869–1870: 487), on the other hand, says for his *S. confervoides*, "spiculis perminutis, ⅔ lin. circ. long.," which is certainly not a *Websteria*. He cites plants from Mauritius and South Africa but none from Madagascar. Clarke (1894: 653) later on also noticed this different sense for which Boeckeler used the name.

Miquel (1847: 225–226) described an *Eleocharis submersus*, which, according to him belongs to that part of the genus which Nees had earlier segregated as

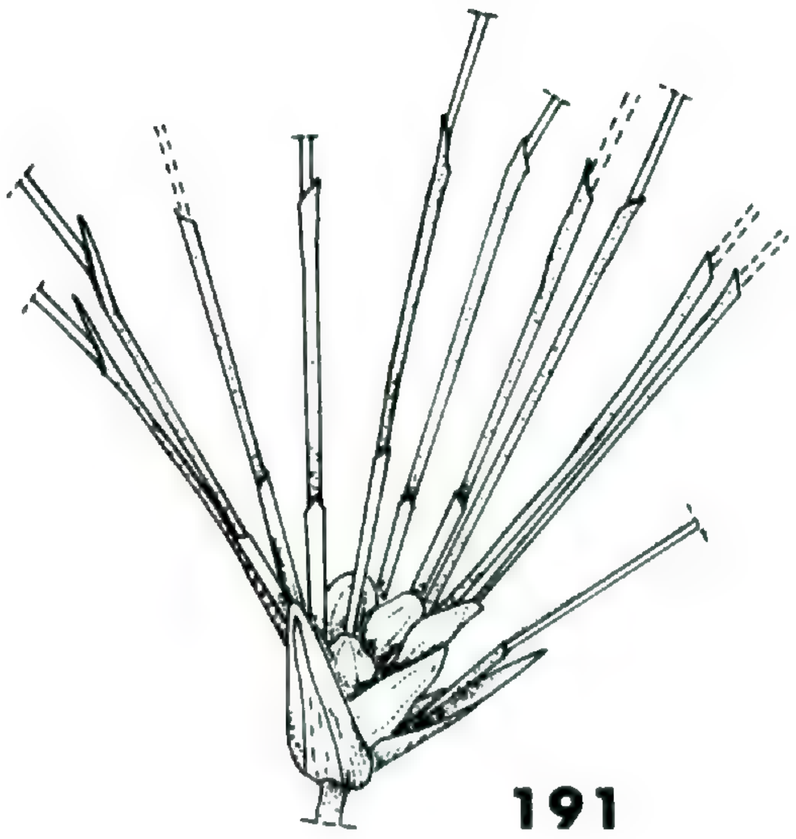
Limnocharis. This use of the epithet "submersus" is previous to and independent of C. Wright's use of it under *Scirpus*, a fact which became confused later on when Durand & Schinz (1895) included Miquel's reference (under the incorrect generic name *Eleogiton*) in their synonymy of *Scirpus submersus*, and Clarke (1900–1901: 91) included it in his synonymy of *S. submersus*. As Süssenguth (1943) later on noted, Miquel's species is not a *Websteria* since the spikelet is described as 3–4 mm long, the lower glumes as "reliquae . . . multinerviae. . . ." and the habit like a flaccid form of *E. capitata*. The only collection cited by Miquel, from Surinam, is referred to as "Crescit ad plant. [ationem] Berlyn, l'Inquietude, sub aqua submersa, m. Sept." Walpers later on (1848–1849: 900) simply copied Miquel's description.

Miquel (1856: 303), in a flora of the East Indies, transferred *Scirpus confervoides* to *Eleocharis* (although with an interrogation) but ascribed the new combination to Kunth (1837: 173). However, Kunth had merely raised the possibility of the Willdenow plant being an *Eleocharis* by stating at the end of his description, "Eleocharidis species?"; Miquel was the first to actually list "confervoides" under *Eleocharis*. However, the collection he cites, *Jungh*, "Java, bij Batavia," may not be a *Websteria*. Miquel himself questions whether it is the same species as the Madagascar plant. Since he says his plant has "foliis longissimus," it is strange he considers it an *Eleocharis*, which does not have leaf blades.

Bentham (1881) published *Rhynchospora ruppioides* with an illustration. The text description was based on *Balansa 2550* from Paraguay and *Thwaites* from near Colombo, Ceylon. Bentham says he could find no difference between the two collections. By its branching, spikelet, flower, fruit and bristles, the plant illustrated is obviously a *Websteria*. Bentham did not relate his species to Poiret's *Scirpus confervoides* nor to the previously published *Scirpus submersus* of Charles Wright. He gave no explicit reason for including the plant in *Rhynchospora*, although it could have been, as Clarke later on (1900–1901) pointed out, because of its 1-fruited spikelet. Bentham described the plant as 1-flowered and with 3–4 glumes, but said these gradually increased [presumably in size] from the short outermost to the flower-bearing innermost ("Glumae 3–4, rigidae, ab extimo brevi ad intimum florentem gradatim auctae"), while Poiret had described the outer glumes as the longest. Also, Bentham twice stated that the species had 6 bristles per spikelet while his illustrations show 10. Therefore, it is possible he examined the spikelets of only the Ceylon specimen and included the Paraguay specimen in the same species from general similarity of habit, but the artist used the Paraguay specimen (which shows only two long glumes) for drawing the spikelets.[4]

In Charles Wright's (1868: 176) previous description of *Scirpus submersus* he mentioned Thwaites's Ceylon specimen which he apparently had seen. He said his own plant had the same habit but a different fruit and therefore was a new species. Since Wright referred to Thwaites's plant as "Sc. ruppioides Thw. e

[4] In a letter to me Ms. Sheila S. Hooper states: "The habit drawing on the *Icones* plate is not an exact reproduction of the whole or part of either syntype—witness the curious thick 'branch' at the left side of the plate. But I think it is mostly taken from CP 3936 [the Thwaites specimen]. It could not have been wholly taken from Balansa 2550 which has no main stem to serve as original for the thick 'branch'."



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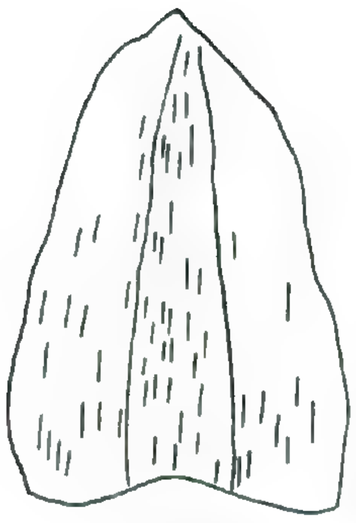

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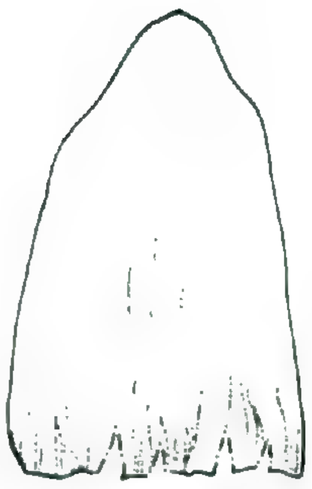

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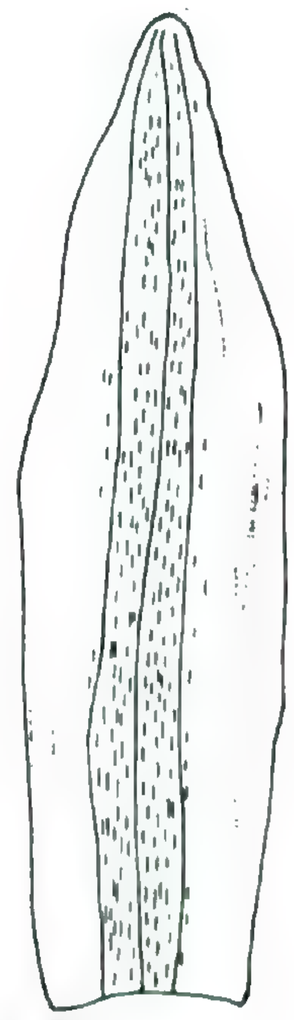

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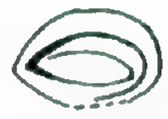

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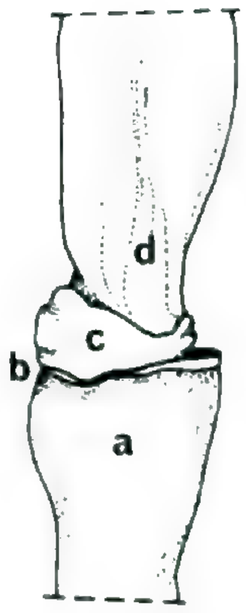

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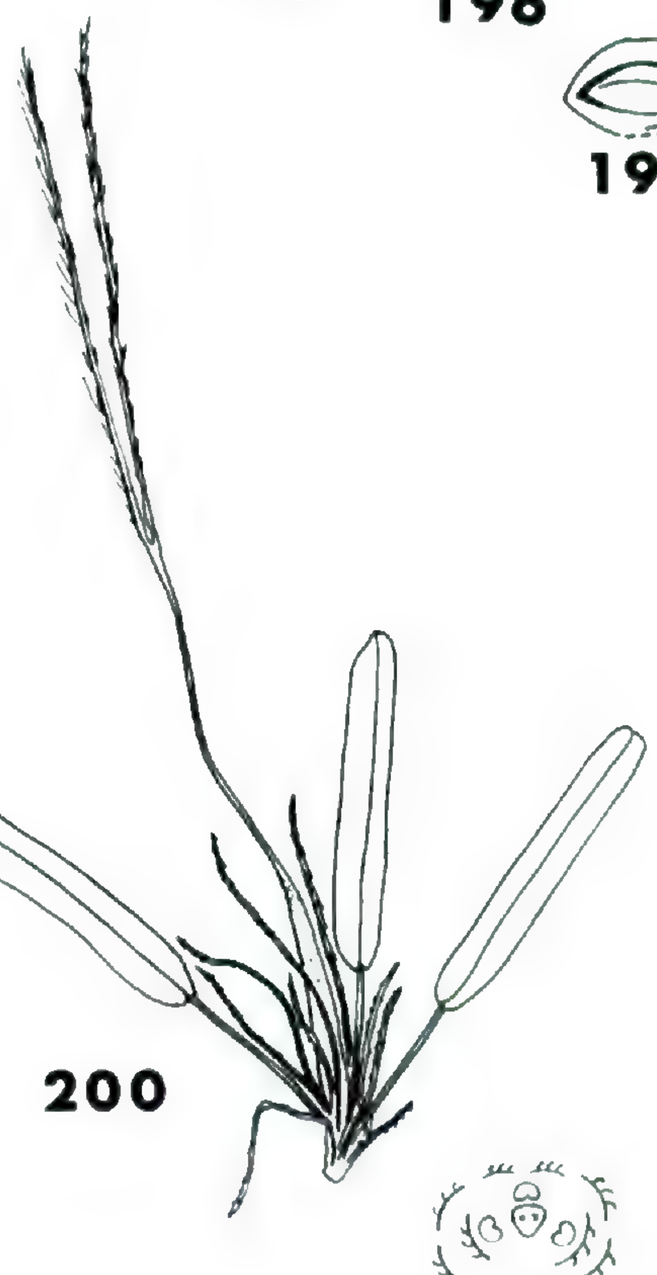

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FIGURES 191–201.—191. Base of a whorl; × 7. Note the two external bracts at base of whorl and the scales (prophylls?) among the culm bases with their two leaf sheaths. Culms shown in dashed lines had decomposed leaving only their empty leaf sheaths.—192. Lower external bract at whorl base; × 17. It is streaked with short dark lines and has a median thicker portion delimited by the two lines shown.—193. Upper external bract at whorl base; × 17. This is of thinner tissue than the lower bract and has no veins.—194. Spikelet with associated scale and glume in natural position; × 7. The associated scale is beginning to open by splitting. The glume inside it is convolute and projects beyond the associated scale.—195.

Ceylon," Thwaites had apparently given his plant a name on the label, a name whose epithet (under *Scirpus*) Bentham used (under *Rhynchospora*).[5] However, since Bentham did not indicate that he was taking the epithet from Thwaites, as well as his putting it under a different genus name, the author of *Rhynchospora ruppioides* is Bentham, as generally admitted, and not Thwaites ex Bentham.

Trimen (1885a: 103, 1885b: 140) cites Bentham's species in his species lists of Ceylon plants, mentioning specimen "C. P. 3936." This is Thwaites's specimen, the "C. P." standing for "Ceylon Plant" and the number being an accession number of the specimen in the Peradeniya Herbarium.

Clarke (1894) noticed the resemblance of the Ceylon plant and the Old World plants in general to Charles Wright's description of *Scirpus submersus*, and in fact used Wright's name for the Ceylon species instead of Poiret's earlier name without giving a reason. He states in synonymy, "S. confervoides *Poir. Encyc.* vi 755 (non Boeck.)," not, of course, because he thinks Poiret's name is a later homonym but because he thinks Boeckeler's use of the name is for another species; apparently he is referring to Boeckeler's 1869–1870 article which I have already mentioned. Clarke cited two Ceylon specimens for his *S. submersus*, *Thwaites* (C. P. 3936), and *Beckett*, and stated that the two lower [outer] glumes were concave and elliptic-oblong, the lower of the two empty and the next with a nut-bearing flower, while the upper glumes were smaller, sterile or bearing a male flower, or sometimes none. This description accords with Poiret's and is different from Bentham's text description.

Durand & Schinz (1895), in their conspectus of the flora of Africa, used the name *Scirpus submersus* and in their synonymy included Poiret's *S. confervoides* and the other names based on Old World plants as well as S. H. Wright's *Websteria limnophila*, but not Britton's new combination, *W. submersa*.

Lindman (1900: 21) lists *Balansa 2550* from Caaguazú, Paraguay, "dans les marais, april, 1876" (the collection Bentham had cited) under *Scirpus submersus* C. Wright. There is no description.

Clarke (1900–1901), under *Scirpus submersus*, gives in synonymy names from Old and New World plants and describes the spikelets as having more than two glumes ("glumis 2 imis 8 mm longis, glumis ceteris brevioribus, paucis masculis

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[5] This supposition was confirmed in Ms. Hooper's letter: "Thwaites had the plant from a Mr. W. Ferguson, who collected it in Colombo in February 1867 and he [Thwaites] wrote 'Scirpus ruppioides' and 'CP 3936' on it. Sketches for the Icones plate dissections are attached to one of the Kew sheets of it which ought to be the lectotype if two species are recognized." Of course, whether *ruppioides* is recognized as a distinct species from *confervoides* or not, the Thwaites specimen, CP 3936, should be chosen as the lectotype for the name *Rhynchospora ruppioides*. Although the drawings are attached to the Ceylon specimen, as stated the spikelet drawing may be from the Paraguay specimen because of the difference in bristle number.

←

Glume spread out, with midvein; × 7.—196. Associated scale spread out, with three veins, the two lateral ones delimiting a thickened median portion; × 7.—197. Cross section of these laminas, in natural position in this spikelet.—198. Dorsal view of an associated scale; × 7.—199. Base of spikelet. a = tip of peduncle; b = scar where associated scale was attached; c = short internode between associated scale and glume; d = base of glume; × 28.—200. Flower; × 7. Filaments have not yet lengthened. Note bristles.—201. Floral diagram of this flower.

(?) aut rudimentariis vel 0"). The only collection he cites is the type, *C. Wright 3775*, but it is not clear if his description, especially as to the number of glumes, is based on original observation of this collection or if it is taken from his former description of the Ceylon plants. Like Poiret, Clarke thinks the species is close to *Scirpus fluitans* L.

Chodat & Hassler (1903: 1019–1020), in their flora of Paraguay, mention the species as *Scirpus submersus*, cite the collections *Balansa 2549*, *2550*, and give *Rhynchospora ruppioides* and *Websteria limnophila* in synonymy. There is no description. The range given for the species is Madagascar, Ceylon, Java, Carolina, Cuba, Surinam, Amazonia Inferior and Paraguay, thus including plants which, as we have seen, are not all *Websteria*.

Chermezon (1937: 143), in his sedge flora of Madagascar, called the species *Scirpus confervoides*. He included *S. submersus* in synonymy but not S. H. Wright's nor Britton's *Websteria*. He cited three collections, that of Petit-Thouars (to whom he referred as Dupetit-Thouars), and two of Perrier de la Bâthie, and stated that the plant has flaccid translucent capillary "leaves" in bunches, the 2 lower glumes 7–10 mm long, the lower of the two sterile and the next fertile, and sometimes 1–2 very small thin upper glumes; generally there is only one fertile flower, rarely two. He gives the general distribution of the species as Gabon, Congo, Madagascar, Java, and tropical and subtropical America.

In Süssenguth's general discussion (1943), he gives the synonyms of both Old and New World plants, but apparently he thinks there are two species (he does not state so definitely) because he says: "Dagegen wird die typische Art von Bentham, Urban und Clarke . . . als eine Pflanze beschreiben, deren Ährchen mehr als 2 Spelzen besitzen," while C. Wright and S. H. Wright described their plants as having only the two long glumes. Since the material he examined from Brazil (and on which he based his two new varieties) has only two glumes in the spikelet, he considered them allied to the Cuba and Florida specimens and therefore used C. Wright's epithet "submersus" for this different species which he accepts as in the independent genus *Websteria*.

León (1946: 204) mentions *Websteria submersa* (Miquel) Britton (a combination never published) for the flora of Cuba but gives only the New World as its general distribution. He mistakenly gives Miquel as the original author of the epithet "submersus" instead of C. Wright. Probably he was thinking of Miquel's (1847: 225–226) *Eleocharis submersa*, which Clarke (1900–1901) cites, although Süssenguth (1943) had stated his belief that this refers to a non-*Websteria*-like species.

Barros (1960) in his sedge flora of Santa Catarina, Brazil, called the species *Scirpus submersus* and included *Rhynchospora ruppioides* and *Websteria limnophila* in synonymy. His illustration is obviously of a *Websteria*. He cites one collection from Santa Catarina and one from Rio Grande do Sul but states that the species also occurs in Paraguay and Missiones (Argentina) although it is not included in his previously published sedge flora of Argentina (Barros, 1947). He gives its general distribution as warm and temperate regions in both hemispheres. He mentions only two glumes for the spikelet.

Hooper (1972), without textual comment, transferred *Scirpus confervoides* to

FIGURE 202. Habit of a sterile submersed plant of an undetermined species of *Eleocharis*; *Luetzelburg 12518*; × 0.5. The branching of this plant slightly resembles that of *Websteria*.

Websteria as a new combination and included only *Rhynchospora ruppioides* as a synonym. Since she did not include *Scirpus submersus*, *Websteria limnophila*, nor *W. submersa* in the synonymy, one could conclude that she considered the Old World plants to be a different species from the New World plants. However, in

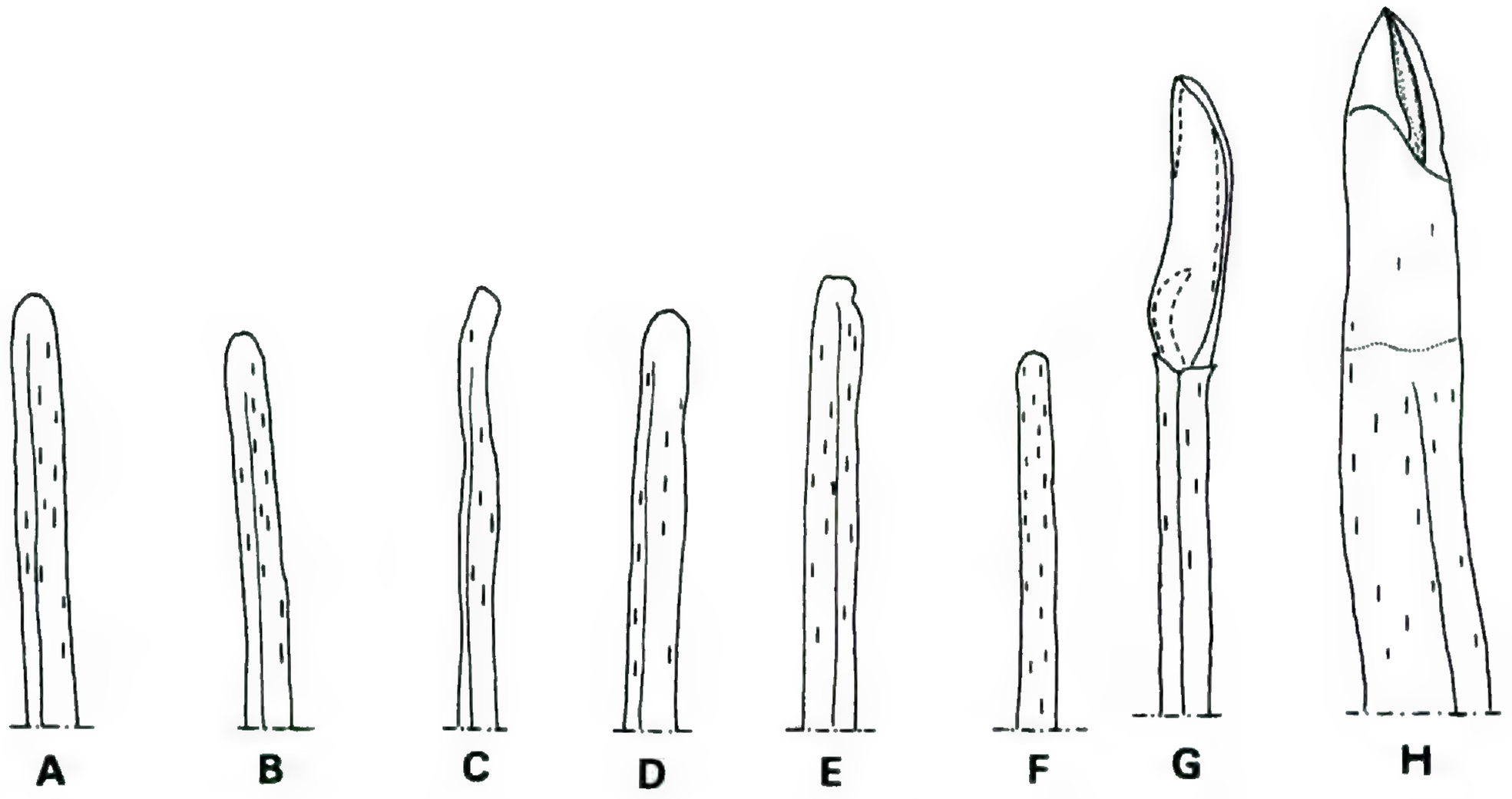

FIGURE 203. Culm tips of *Websteria*, A–F, and *Eleocharis*, G–H; × 40. In *Websteria* the culm apex lacks bracts; in *Eleocharis* spp. they are always covered by enrolled scalelike bracts.—A. *Pires et al. 3606*.—B. *Fróes 32156*.—C. *C. Wright 3775*.—D. *Luetzelburg 271*.—E. *Martius 2810*.—F. *Luetzelburg s.n.*, Oct. 1927.—G. *Luetzelburg 12518*.—H. *Luetzelburg 15051*. (Also see culm tips of *Eleocharis* species in Figs. 25, 65, 74–75.)

answer to an inquiry of mine about this, she stated that she thought they were all one species.

As mentioned, Hooper later on (1973), in a key to the genera of Cyperaceae for the world, sunk *Websteria* in *Eleocharis*. However, her letter to me stated that this was a previous opinion of hers which, since it was to appear in the third edition of Hutchinson's *Families of Flowering Plants*, was held up in its publication until this book was published. Her present opinion is that of her 1972 paper, that *Websteria* is a separate genus.

Thus, up to now, New World authors with the exception of Barros have not taken the Old World plants or the names based on them into consideration. Since Wright's publication of *Scirpus submersus*, the European authors (and Barros) have taken the New World plants and at least some of the names based on them into consideration but, with the exception of Süssenguth, have assumed that only one species was involved. Of these later authors, some put the species in *Scirpus* and some in *Websteria*, some used *confervoides* as the specific epithet and some, *submersus*, in the latter case without giving any reason why they used the later epithet.

I have examined one collection of *Websteria* from the Old World (Botswana, Northern District, Gobegha Lagoon, Okavango Swamp, 23°15′E 19°10′S, 1000 m, 5 March 1972, *Gibbs Russell & Biegel 1502*), and as far as I can make out, it is identical to the many I have seen from the New World. It has ripe fruits with bristles which look like the fruits of the New World plants illustrated in this paper. The fruit body color is a smooth shining ivory; the cells of the surface are not easily visible except those on the stylebase which have a slight tendency to be hexagonal. The ripe fruit examined was 3.5 mm tall, including the style-

base, and 1.7 mm wide, and had 11 bristles. The spikelets of this collection have only two large laminas (the associated scale and glume) and no smaller glumelike laminas outside or inside the large ones. These large laminas are a lightly purplish straw color, delicately streaked with purple lines. In one of the spikelets examined the associated scale was 8.7 mm long and the glume 11 mm long. The peduncles were unusually long, 7.8–9 cm, and 0.3 mm wide. The delicate sheath at the base of the peduncle was 21 mm long.

Since at least one Old World collection is plainly identical to the New World *Websteria*, it seems best to consider the whole genus as presently known to consist of one species. More Old World material would have to be examined to check on the reality of the presence of extra small "glumes" or more than one flower, but even if these really do occur but are not correlated with any other consistent morphological differences, they could be considered as vestiges of reduction such as are sometimes found in some but not all individuals of a species, without necessarily even calling for the creation of varieties. In any case there does not seem to be two distinct species. Bentham, as stated, also saw material from both the Old and New Worlds and considered them the same species.

As for the correct specific epithet, although I have not seen the type of *Scirpus confervoides*, we may provisionally use this epithet for the time being.

Websteria has always been described as having whorled filiform leaves (Poiret, 1804; C. Wright, 1868; S. H. Wright, 1887; Clarke, 1894, 1900–1901; Süssenguth, 1943). Actually, all of these "leaves" are filiform culms. The only organs of foliar tissue that *Websteria* possesses are the sheaths at the base of the culms and peduncles, the two basal external bracts of the whorls, the prophylls among the culms, the associated scale and the glume.

Some sterile collections from the Munich herbarium which I examined, *Luetzelburg 12518, 12528*, and *15051*, had been determined and were cited by Süssenguth as *Websteria submersa*. However, they are species of *Eleocharis* with a submerged-aquatic habit. The distinction between *Websteria* and *Eleocharis* is easily made considering the size of the associated scale and glume and usually the number of flowers in the spikelets. When the material is sterile, the two genera can be distinguished by the branching pattern (Eiten, 1964). But sometimes aquatic specimens of *Eleocharis* have a vegetative growth that approximates (but does not equal) that of *Websteria* (Fig. 202). However, the two genera can always be distinguished by examining those culm tips that do not bear whorls or spikelets. In all species of *Eleocharis* the culm apices are covered over by scalelike bracts (Eiten, 1969), while in *Websteria* there are no bracts visible; the apex is bare (Fig. 203).

Other collections examined (det. L. T. Eiten):

Websteria confervoides (Poiret) Hooper

UNITED STATES. FLORIDA: Volusia Co., lake SE of Lake Helen, Dec. 1886, *S. H. Wright s.n.* (US, syntype of *Websteria limnophila* S. H. Wright).

CUBA. *C. Wright 3775* (NY, US ex herb. Canby). PINAR DEL RIO: San Luiz, Laguna de Sancta Maria Chica, 20 May 1944, *Victorin & Alain* (NY).

TRINIDAD. Aripo Savanna, 8 Nov. 1961, *Richardson 2016* (NY).

GUYANA. Upper Mazarini River, 22 Sep.–6 Oct. 1922, *de la Cruz* (US).

BRAZIL. PARÁ: Mun. de Prainha, cabeceira do Rio Uruará, 3 June 1955, *Fróes 31936*

(IAN). Santa Izabel (40 km de Belém), 7 July 1968, *Pires 11879* (IAN). Lago do Macapichi, 1 Dec. 1955, *Fróes 32156* (IAN). Serra do Cachimbo, 425 m, 15 Dec. 1956, *Pires et al. 6306* (IAN). BAHIA: Rio das Contas, *Luetzelburg 271* (M).

I regard the sheet of *Luetzelburg s.n.*, Paren-intôe, Serra do Sol, Oct. 1927, (M), which had been marked as "Typus variet," as the holotype of var. *luetzelburgii*, the other sheet and the sheet with a fragment as isotypes.

All three sheets of *Martius 2810* were marked as var. *negrensis* by Süssenguth without stating which he considered the holotype. The first specimen has written on the bottom of the sheet: "Aetia brasiliensis Mart. Obs. n° 2810. Barra do Rio Negro. Novbr. 1819. Obs. n° 2810." The second sheet says: "Aëtia brasiliensis Mart. n° 2810." The third says: "Aetia brasiliensis Mart. Obs. n° 2810. Barra do Rio Negro 1820." I hereby chose the first sheet as lectotype. The others become isolectotypes. Martius's name, "Aëtia brasiliensis," was never published, which is a pity for he was the first to recognize this genus as independent.

LITERATURE CITED

BALLARD, F. 1934. *Rhynchospora confusa* Ballard. Hooker's Icon. Pl. 33: *tab. 3250*, 3 pp.

BARROS, M. 1947. *In* H. R. Descole, Genera et Species Plantarum Argentinarum. Vol. 4 (2 parts). Institutionis Michaelis Lillo, Buenos Aires.

———. 1960. Las Ciperaceas del Estado de Santa Catalina. Sellowia 12: 181–450, *116 figs.*

BENTHAM, G. 1881. *Rhynchospora ruppioides* Benth. Hooker's Icon. Pl. 14: 31–32, *pl. 1344.*

BOECKELER, O. 1869–1870. Die Cyperaceen des Königlichen Herbariums zu Berlin. Linnaea 36: 271–690.

BRITTON, N. L. 1888. New or noteworthy North American phanerogams—I. Bull. Torrey Bot. Club 15: 99–100.

CHERMEZON, H. 1937. Cypéracées. *In* H. Humbert, Flore de Madagascar. Gouvernement Général de Madagascar, Tananarive.

CHODAT, R. & E. HASSLER. 1903. Plantae Hasslerianae. Bull. Herb. Boissier, sér. 2, 3: 1007–1039.

CLARKE, C. B. 1894. *In* J. D. Hooker, Flora of British India. Vol. 6. L. Reeve & Co., London.

———. 1900–1901. Cyperaceae. *In* I. Urban, Symbolae Antillanae. Vol. 2: 8–162. Fratres Borntraeger, Lipsiae.

———. 1909. Illustrations of Cyperaceae. Williams & Norgate, London.

DURAND, T. & H. SCHINZ. 1895. Conspectus Florae Africae. Vol. 5. Jardin Botanique de l'État, Bruxelles.

EITEN, L. T. 1961. Sôbre o estado autônomo do gènero *Helonema* (Cyperaceae). Resumo. Anais XII Reunião Anual Soc. Bot. Brasil. São Paulo. Pp. 20–22.

———. 1964. *Egleria*, a new genus of Cyperaceae from Brazil. Phytologia 9: 481–487.

———. 1969. Vegetative anatomy of *Eleocharis interstincta* (Vahl) Roem. & Schult. Arq. Bot. Estado São Paulo 4: 187–228.

———. 1970. Notes on Brazilian Cyperaceae—II. Phytologia 20: 273–276.

———. 1972. Name change for *Eleocharis pygmaea* (Süss.) L. T. Eiten. Phytologia 22: 423.

———. 1976. Inflorescence units in the Cyperaceae. Ann. Missouri Bot. Gard. 63: 81–112.

HOOPER, S. S. 1972. New taxa, names and combinations in Cyperaceae for the 'Flora of West Tropical Africa'. Kew Bull. 26: 577–583.

———. 1973. Keys to genera of Cyperaceae. *In* J. Hutchinson, The Families of Flowering Plants. Ed. 3. Clarendon Press, Oxford.

HUTCHINSON, J. 1959. The Families of Flowering Plants. Ed. 2. Vol. 2. Monocotyledons. Clarendon Press, Oxford.

KOYAMA, T. 1967. Cyperaceae-Mapanioideae. Mem. New York Bot. Gard. 17: 23–79.

——— & F. H. F. OLDENBURGER. 1971. *Diplacrum africanum* newly found in tropical America. Rhodora 73: 159–160.

KUNTH, C. S. 1837. Enumeratio Plantarum. Vol. 2. J. G. Cottae, Stuttgardiae.

LEÓN, H. 1946. Flora de Cuba. Vol. 1. Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 8: 1–441.

Lindman, C. A. M. 1900. List of Regnellian Cyperaceae collected until 1894. Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26(III, 9): 1–41, 8 *pls.*

Miquel, F. A. G. 1847. Symbolae ad Floram Surinamensem. Pars IX. Continuatio plantarum Fockeanarum: Cyperaceae, Rapateae. Linnaea 19: 221–233.

———. 1856. Flora Indiae Batavae. Vol. 3. Amsterdam. [1855 on title page.]

Pfeiffer, H. 1925. *Syntrinema*, genus novum Cyperacearum Brasiliensium. Repert. Spec. Nov. Regni Veg. 21: 238–240.

Poiret, J. L. M. 1804. *In* J. B. A. P. M. Lamarck, Encyclopédie Méthodique. Botanique. Vol. 6. Paris.

Schultze-Motel, W. 1959. Entwicklungsgeschichtliche und vergleichend-morphologische Untersuchungen im Blütenbereich der Cyperaceae. Bot. Jahrb. Syst. 78: 129–170, *Taf. 4–5.*

Süssenguth, K. 1943. Einige neue Gattungen und Arten der Cyperaceae aus Südamerika. Bot. Jahrb. Syst. 73: 113–125.

———. 1952. Kurzer Bericht über eine Arbeit von L. Bittl, Anatomische Studien an der Gattung *Chamaegyne* Suesseng. (Cyperaceae). Mitt. Bot. Staatssamml. München 4: 119.

Svenson, H. K. 1937. Monographic studies in the genus Eleocharis—IV. Rhodora 39: 210–231, 236–273.

Torrey, J. 1836. Monograph of North American Cyperaceae. Ann. Lyceum Nat. Hist. New York 2: 239–448.

Trimen, H. 1885a. Systematic Catalogue of the Flowering Plants and Ferns Indigenous to or Growing Wild in Ceylon. Government Printer, Colombo.

———. 1885b. Notes on the flora of Ceylon. J. Bot. 23: 138–145.

Troll, W. 1964. Die Infloreszenzen: Typologie und Stellung im Aufbau des Vegetationskörpers. Band I. Gustav Fischer Verlag, Stuttgart.

Walpers, G. G. 1848–1849. Ann. Bot. Syst. 1: 900.

Wright, C. 1868. *In* F. A. Sauvalle, Flora Cubana. Havana. [1873 on title page.]

Wright, S. H. 1887. A new genus in Cyperaceae. Bull. Torrey Bot. Club 14: 135.

CYTOTAXONOMIC STUDIES IN THE TRIBE QUILLAJEAE (ROSACEAE)[1]

PETER GOLDBLATT[2]

ABSTRACT

The following chromosome numbers were found in previously uncounted genera of Quillajeae: $n = 17$ in *Lindleya* and *Kageneckia*, and $n = 15$ in *Vauquelinia*. An earlier count of $n = 27$ in *Lyonothamnus* is confirmed, but *Quillaja*, previously reported as $n = 17$ is shown to have $n = 14$ in both species currently recognized. This variety of chromosome numbers supports the widely held contention that the tribe is unnatural. *Lindleya* is regarded here as a member of the Maloideae, where $x = 17$ is basic, and *Vauquelinia* is suggested as best placed in this subfamily. The genus *Exochorda*, known to have $n = 8$, appears to accord with Prunoideae ($x = 8$), particularly with *Oemleria*, while *Lyonothamnus* seems best left in Spiraeoideae ($x = 9$). The peculiarities of the remaining genera, *Kageneckia* and *Quillaja*, suggest that they be placed in a separate subfamily.

Traditionally the Rosaceae have been treated as comprising six subfamilies, or as in more recent treatments four, with the Neuradoideae and Chrysobalanoideae recognized as distinct families. The remaining subfamilies, Spiraeoideae, Prunoideae, Maloideae and Rosoideae, are by and large natural groupings and, as might be expected from so ancient and comparatively primitive dicot group, relatively distinct from one another. This classical treatment of the family is supported by chromosomal data. The basic chromosome number in the family appears almost certainly $x = 9$ (Raven, 1975) and this base number is found in the Spiraeoideae (with several notable exceptions) usually regarded as the least specialized of the four subfamilies with its partly to completely free carpels and dry, usually follicular fruits. In the subfamily Prunoideae the base number is $x = 8$, in the Maloideae, $x = 17$ (clearly a palaeotetraploid group), and while a base number of $x = 7$ predominates in the Rosoideae, $x = 9$ and $x = 8$ also occur in several lines.

The Spiraeoideae appear to be the least homogeneous of the rosaceous subfamilies, the discordant elements being a number of genera usually placed in the tribe Quillajeae, which have in common dry, dehiscent fruits with winged seeds. In its broadest sense (Hutchinson, 1964) the tribe comprises the following genera: *Quillaja*, *Kageneckia*, *Vauquelinia*, *Lindleya*, *Exochorda*, and *Lyonothamnus*. The last-mentioned is included only by Hutchinson and differs in having two to three carpels in contrast to five in the other genera, and, in spite of statements to the contrary, its seeds are not winged. Various authors since Spach

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(1834: 429), who excluded the Quillajeae from the Spiraeoideae, have implied or stated that the tribe is not a natural alliance. Schulze-Mentz (1964), for example, admits only *Quillaja*, *Kageneckia* and *Vauquelinia*, while placing *Exochorda* and *Lindleya* in the Exochordeae and *Lyonothamnus* in the Sorbarieae. Certainly, differences between some genera of the Quillajeae seem greater than between other tribes and even subfamilies of the Rosaceae. This is reflected in what little has been known of the cytology of the group with reported chromosome numbers in three genera ranging from $n = 27$ ($x = 9$?) in *Lyonothamnus*, $n = 7$ in *Quillaja*, and $n = 8$ in *Exochorda* (Table 1), the latter genus already associated with the Prunoideae because of its cytology (Raven, 1975). Thus cytological data amplifies the likelihood that the alliance is unnatural.

The present study was undertaken in the hope that a more comprehensive knowledge of the cytology of the tribe will lead to a better understanding of the affinities of the genera placed in the Quillajeae and of the overall evolution in the Rosaceae.

Cytology

Chromosome counts were made either from anther squashes or root tips, and counts (Table 1) are accordingly reported as gametic or somatic. Fixed buds for meiotic study were either collected from wild plants, in the case of *Lindleya* and *Vauquelinia corymbosa*, or from cultivated material from a known wild source, *Kageneckia oblonga*, *K. angustifolia*, and *Quillaja saponaria*. Mitotic studies were made from root tips collected from germinating seeds grown at the Missouri Botanical Garden. Seeds of *Kageneckia lanceolata* and *Vauquelinia angustifolia* were collected from wild plants, while seed of *Quillaja brasiliensis* and *V. californica* were obtained from plants in cultivation.

Buds were fixed in 1:3 acetic:ethanol and stained in propionic carmine. Root tips were pretreated either in hydroxyquinoline or 0.1% colchicine for 4 hours, fixed, macerated in 10% HCL for 4 minutes and squashed in lactopropionic orcein.

The results presented in Table 1 are briefly summarized as follows. All species of *Vauquelinia* studied have a chromosome number of $n = 15$, the three species of *Kageneckia* have $n = 17$, and the monotypic *Lindleya* has $n = 17$. The report for two species of *Quillaja*, both $n = 14$, is in sharp contrast to the previous report for this genus, $2n = 34$ (Bowden, 1945). Bowden's report was for *Q. brasiliensis*, also studied here, and in the light of the present records of $n = 14$ in two species of *Quillaja*, Bowden's count can only be viewed with misgiving. It was probably based on material of some species of Maloideae, and no voucher seems to exist.

The previous report on $n = 27$ for *Lyonothamnus* (Raven et al., 1965) is confirmed here, for the same subspecies, subsp. *asplenifolius*. The tentative count of $2n = 48$ (Stebbins & Major, 1965) in *L. floribundus* thus was only approximate, as suggested by Raven et al. (1965). The only genus of the tribe not examined in the present work, *Exochorda*, is known to have $n = 8$ (Table 1).

Discussion

With each of the four subfamilies of the Rosaceae (excepting the tribe Quillajeae) having a different and characteristic base number, the variation in

TABLE 1. Chromosome numbers in the tribe Quillajeae sensu lato. Whenever known, complete collection data and voucher information is presented. Counts determined during this investigation in **bold face**.

Species	Chromosome No. Gametic	Somatic	Collection Data and/or Author Citation
Exochorda			
giraldii Hesse	8		(Sax, 1931: cult. Arnold Arboretum, Cambridge, Mass.; collection data not known, no voucher kept).
tianschanica Gontsch.	8		(Federov, 1969).
Kageneckia			
angustifolia D. Don	**17**		Cult. Carnegie Inst. of Washington, Stanford, Calif.; seed ex Chile, Prov. Santiago, Yeso Valley, *Mooney SA80* (DS).
lanceolata R. & P.	**17**		Cult. Missouri Botanical Garden; seed ex Peru, Dept. Ayacucho, San Juan de Lucanas, *Ketcham 80* (MO).
oblonga R. & P.		**34**	Cult. Carnegie Inst. of Washington, Stanford, Calif.; seed ex Chile, Quebrada de la Plata, *Mooney SA73* (DS).
Lindleya			
mespiloides H.B.K.	**17**		Mexico, Querétaro, near Maconi, *Rzedowski 31605* (ENCB).
Lyonothamnus			
floribundus Gray		48	(Stebbins & Major, 1965: cult. Berkeley, Calif.; ex California, Santa Cruz Island).
floribundus subsp. *asplenifolius* (Greene) Raven	27		(Raven et al., 1965: cult. Rancho Santa Ana Botanic Garden, Claremont, Calif.; ex California, Santa Cruz Island, *Wolf 4129* (RSA) progeny.
	27		Collection data same as above.
Quillaja			
brasiliensis (St. Hil.) Mart.	17		(Bowden, 1945: seed ex Botanical Garden, Montevideo, Uruguay, no voucher kept).
		28	Ex hort. Station de Botanique et de Pathologie Vegetale, Antibes, France.
saponaria Mol.	**14**[a]		Cult. Univ. of California Botanical Garden, Berkeley, Calif.; seed ex Chile, Prov. Santiago, Maipú Valley, *West 6010* (UC).
Vauquelinia			
cf. *angustifolia* Rydb.		**30**	Mexico, Chihuahua, near Coyama *Wendt et al. 9841* (MO).
		30	Mexico, Chihuahua, Sierra de Chrysaderos, *Johnston 8907* (TEX).
californica Sarg.		**30**	Ex hort. C. T. Mason, Arizona, *Mason s.n.* (MO).
corymbosa Correa	**15**		Mexico, Hidalgo, Atotonilco el Grande, *Rzedowski 31515* (ENCB).

[a] Count made by G. Davidse, Botany Department, Missouri Botanical Garden.

chromosome number within the Quillajeae appears all the more startling. If the Quillajeae is regarded in its broadest sense (Hutchinson, 1964), this single tribe is as heterogeneous chromosomally as the whole family Rosaceae. However, it is clear that the tribe cannot be considered a natural alliance and some genera at least can be reclassified with some degree of confidence in the light of the cytological evidence.

EXOCHORDA

The concurrence of the base number of *Exochorda*, $x = 8$, with that of the Prunoideae suggests this as a more suitable taxonomic position, though at first glance the 5-carpellate ovary and dry, capsular fruit of *Exochorda* seem misplaced in the Prunoideae. However, comparison with the isolated prunoid genus, *Oemleria* (*Osmaronia*), unusual in having a 5-carpellate drupaceous fruit, brings to light a number of similarities. Both *Exochorda* and *Oemleria* have obsolete stipules and a similar 5-carpellate ovary with two epitropic ovules, the latter condition a characteristic though not unique prunoid condition.

Exochorda, the only member of the Quillajeae which has a base number at the diploid level, does in fact seem particularly misplaced in this tribe and its transfer to the Prunoideae appears warranted. Sterling (1969) has pointed out that *Oemleria* is anatomically rather isolated from other members of the Prunoideae and proposed segregating it as a distinct tribe, Osmaronieae. The inclusion of *Exochorda* in this tribe, within the Prunoideae, may be the most satisfactory way to reflect the natural relationships of the genus.

LINDLEYA

Since *Lindleya* has the same base number, $x = 17$, that is characteristic of the Maloideae, its association with the Quillajeae and the Spiraeoideae appears highly questionable. Of fundamental importance is the validity of the traditional distinction between the two subfamilies. Maximowicz (1879) considers the pome, with its fleshy receptacle, the only difference between the Maloideae and Spiraeoideae. With certain Quillajeae excepted, the free carpels of the Spiraeoideae provide a second important difference between the subfamilies. Since the spiraeoid base number, $x = 9$, invariably is linked with free carpels, and the maloid base number, $x = 17$, is associated with a fleshy and syncarpous fruit, *Lindleya* may well be better placed in this latter group, even though it has a dry fruit. Sterling (1966) has commented that the carpels of *Lindleya* are fused in the manner very characteristic of the Maloideae. Other authors also have associated *Lindleya* with this subfamily on anatomical grounds, notably Bonne (fide Sterling, 1966), who strongly links *Lindleya* with *Mespilus*. There is also phytochemical evidence linking *Lindleya* with the Maloideae since the phenolic, isochlorogenic acid (Challice, 1973) found in many Maloideae, occurs in *Lindleya* and in no other Spiraeoideae. Challice (1974) has, however, found that the chemotaxonomically significant flavone C-glycosides found in many, but not all, Maloideae are absent in *Lindleya*.

There is obviously a strong argument to be made for considering genera such

as *Lindleya* intermediate between the Spiraeoidea and Maloideae, and it certainly has morphological and chemotaxonomic features of both. However, the very characteristic base number, $n = 17$, makes it appear that the affinities of *Lindleya* lie with the Maloideae rather than with the Spiraeoideae. Transfer of *Lindleya* to the Maloideae is perhaps the best taxonomic solution to the problem.

KAGENECKIA

With cytology of all three species in the genus known, it is evident that *Kageneckia*, with $n = 17$, has the same base number as that occurring in the Maloideae. It is, however, difficult to envisage a close relationship between *Kageneckia* and this subfamily. Its carpels are free (confirmed anatomically by Sterling, 1966), and contain many predominantly pleurotropic ovules, whereas the ancestral condition for the Maloideae is probably biovulate (Sterling, 1969). There is, however, some resemblance between the carpels of *Kageneckia* and those of the multiovulate maloid genera such as *Cydonia*. The possibility that this is a reflection of phylogenetic relationship is perhaps enhanced by the concurrence of basic chromosome number, but nevertheless seems unlikely, unless the Maloideae are regarded as polyphyletic, having originated from ancestral lines with dry, biovulate, syncarpous and multiovulate, apocarpous gynoecia. Chemotaxonomic evidence, although negative, (Challice, 1974) makes it even more unlikely that *Kageneckia* is related to this group of Maloideae as it lacks the characteristic isochlorogenic acid and flavone C-glycosides found in many maloid genera.

Kageneckia exhibits considerably greater resemblance to the other South American member of the alliance, *Quillaja*, which the present study indicates has $n = 14$. The two have similar carpels (although in *Quillaja* they are partly united) and remarkably similar fruits and seeds. The morphological similarities between these two genera are such that it seems most likely that they are indeed related, notwithstanding the impressive differences in basic chromosome number and in chemistry, with the significant flavone C-glycosides occurring in *Quillaja* but not in *Kageneckia* (Challice, 1974).

QUILLAJA

Both species of *Quillaja* have $n = 14$, despite Bowden's (1945) earlier record to the contrary. The base number $n = 14$ for the genus contrasts strikingly with $n = 17$ for *Kageneckia*, probably its closest ally, and it is equally discordant either with the Spiraeoideae or Maloideae (a concurrence with the most common base number, $x = 7$, in the Rosoideae must be regarded as coincidental, and of no phylogenetic significance).

The partly united carpels of *Quillaja* appear to differ only to a small degree from those of *Kageneckia* and in my opinion these two genera are relatively primitive in the Rosaceae. The peculiar and very primitive flavonoid chemistry of *Q. saponaria*, described by Bate-Smith (1965), also supports this contention. Leucodelphinidin occurs only in this species and in the rest of the Rosaceae only in one species of *Potentilla*.

The South American distribution of *Quillaja* and *Kageneckia* contrasts with a predominant Northern Hemisphere distribution for the Rosaceae, and the presence of an ancestral stock in South America suggests the possibility that the family, now poorly represented in the southern continents, may have once been more developed there. The family may have had its origin in West Gondwanaland, i.e., South America and Africa, away from the region of its present concentration, or it may have arrived in South America very early, perhaps via Africa (Raven & Axelrod, 1974), though *Kageneckia* and *Quillaja* have no close relatives in that continent today.

Quillaja and *Kageneckia* appear to represent an ancient line, perhaps derived from spiraeoid ancestors collaterally with the Maloideae. With its partly united carpels *Quillaja* would appear more specialized than *Kageneckia*, and this perhaps accords with its lower base number, $x = 14$, if $x = 9$ is indeed primitive for the family.

VAUQUELINIA

The affinities of this Mexican and southwestern United States genus of small trees are particularly problematic since its base number, $x = 15$, is unique in the Rosaceae. It has 5 biovulate carpels united in the maloid manner, and the apotropic ovules also accord with those of the Maloideae. Except for its different chromosome number, *Vauquelinia* would accord almost as well as *Lindleya* with the Maloideae morphologically, though there appear to be no chemotaxonomic links between *Vauquelinia* and the Maloideae.

Vauquelinia is sometimes associated with the California Island endemic *Lyonothamnus*, which has $n = 27$ (and probably $x = 9$), a relationship strongly supported by Banwar (1966). Several disparities must however be noted. First, *Lyonothamnus*, with unusual opposite leaves, has two (or three) free carpels each with several epitropic ovules. Second, the seeds differ; those of *Lyonothamnus* lack the wing found in *Vauquelinia* and other Quillajeae. In fact, *Lyonothamnus* accords well with the Spiraeoideae, particularly in critical floral and fruit characteristics. With its presumed base number the same as that of the Spiraeoideae, *Lyonothamnus* appears best treated as a rather isolated genus in this subfamily and not closely associated with *Vauquelinia*. On present evidence it appears best to regard *Vauquelinia* as most closely related to *Lindleya* and thus falls marginally into the Maloideae. It is however sufficiently discordant here, both chromosomally and morphologically, that it is only with hesitation that I suggest it be assigned to the Maloideae. Further investigation of this curious genus may bring to light more information on the relationships.

Conclusion

The cytology of the tribe Quillajeae lends considerable support to the belief that this is an unnatural alliance and that most of its constituent genera are misplaced in the Spiraeoideae, a group otherwise characterized by free carpels and dry fruits and a basic chromosome number of $x = 9$. The following changes in taxonomy of the Rosaceae are proposed: *Exochorda* is assigned to the Prunoideae-

Osmaronieae; *Lindleya* and *Vauquelinia* to the Maloideae; and *Lyonothamnus* to the Spiraeoideae, perhaps in a separate tribe. In the light of these changes, the subfamilies of the Rosaceae all require limited redefinition. The Maloideae, with $x = 17$ (and 15 in *Vauquelinia*), have carpels united to one another and to the receptacle and have usually fleshy pomes, but also capsular fruits. The latter condition is perhaps ancestral. In the Prunoideae, with $x = 8$, the drupaceous fruit is characteristic but not definitive, the carpels are free to united but not to the receptacle, and the fruit is a capsule or drupe. In Spiraeoideae, with $x = 9$, the carpels are free and the fruit is a follicle (or achene).

This leaves *Quillaja* and *Kageneckia* unaccounted for and they are perhaps best regarded as constituting a distinct subfamily, developed collaterally with the Maloideae from an ancestral spiraeoidlike stock, and retaining many ancestral characteristics. Cytological and chemotaxonomic data suggest that these two genera are not particularly closely allied, yet morphological similarities dictate their inclusion in the same subfamily or tribe.

LITERATURE CITED

BANWAR, S. C. 1966. Morphological and anatomical studies on the genus *Lyonothamnus*. Ph.D. dissertation. University of California, Berkeley.

BATE-SMITH, E. C. 1962. The phenolic constituents of plants and their taxonomic significance I. Dicotyledons. J. Linn. Soc. Bot. 58: 95–173.

———. 1965. Investigation of the chemistry and taxonomy of sub-tribe Quillajeae of the Rosaceae using comparisons of fresh and herbarium material. Phytochemistry 4: 535–539.

BOWDEN, W. 1945. A list of chromosome numbers in the higher plants. II. Menispermaceae to Verbenaceae. Amer. J. Bot. 32: 191–201.

CHALLICE, J. S. 1973. Phenolic compounds of the subfamily Pomoideae: a chemotaxonomic survey. Phytochemistry 12: 1095–1101.

———. 1974. Rosaceae chemotaxonomy and the origins of the Pomoideae. Bot. J. Linn. Soc. 69: 239–259.

FEDEROV, A. A. (editor). 1969. Chromosome Numbers of Flowering Plants. Izdatel'stvo Nauka, Leningrad.

HUTCHINSON, J. 1964. The Genera of Flowering Plants. Vol. 1. Clarendon Press, Oxford.

MAXIMOWICZ, C. J. 1879. Adnotationes de Spiraeaceis. Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 105–261.

RAVEN, P. H. 1975. The bases of Angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62: 724–764.

——— & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

———, D. W. KYHOS & A. J. HILL. 1965. Chromosome numbers of spermatophytes, mostly Californian. Aliso 6: 105–113.

SAX, K. 1931. The origin and relationships of the Pomoideae. J. Arnold Arbor. 12: 3–22.

SCHULTZE-MENTZ, E. K. 1964. Rosales. *In* H. Melchior (editor), A. Engler's Syllabus der Pflanzenfamilien. Ed. 12. Vol. 2: 193–243.

SPACH, M. E. 1834. Histoire Naturelle des Végéteaux. Vol. 1. Librairie Encyclopédique de Roret, Paris.

STEBBINS, G. L. & J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35: 1–35.

STERLING, C. 1966. Comparative morphology of the carpel in the Rosaceae. IX. Spiraeoideae: Quillajeae. Sorbarieae. Amer. J. Bot. 53: 951–960.

———. 1969. Comparative morphology of the carpel in the Rosaceae. X. Evaluation and summary. Oesterr. Bot. Z. 116: 46–54.

CHROMOSOME NUMBER IN *GOMORTEGA KEULE*[1]

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ABSTRACT

Gomortega keule (Mol.) I. M. Johnston of the monotypic Chilean family Gomortegaceae (Magnoliales sensu lato) has a diploid number of $2n = 42$. This number, indicating the palaeohexaploid nature of the family, suggests affinities with those magnoliaceous families with similar high basic chromosome numbers, in particular Atherospermataceae, Siparunaceae, and Monimiaceae belonging to the lauralian alliance. Morphological features such as endospermous seeds, valvate anthers, as well as wood anatomy and pollen, accord with this conclusion.

Plants referred to *Gomortega keule* and reported as $n = 12$, $2n = 24$ (Raven et al., 1971), have been redetermined as *Bielschmiedia berteroana* (Gay) Kostermans (Lauraceae; Raven, 1975). The chromosome number in *Gomortega* of the monotypic family Gomortegaceae has thus remained unknown until now, and the family is the last in Magnoliales to be counted. The present record thus corrects a past error in the literature and fills a notable gap in the knowledge of cytology in the primitive dicots.

MATERIALS AND METHODS

Seedlings grown by Dr. Schlegel-Sachs of the Universidad Austral de Chile, from seed collected in the wild, were sent to the Missouri Botanical Garden where root tips were collected from the reestablished plants. Root tips were pretreated in hydroxyquinoline for five hours at room temperature, fixed briefly in 1:3 acetic-ethanol, hydrolyzed in 10% HCl at 60° C for 4 minutes, and squashed in lacto-propionic orcein.

Gomortega keule (Mol.) I. M. Johnston. $2n = 42$. CHILE. PROV. CONCEPCIÓN: Near Penco, *Schlegel-Sachs 6418* (MO).

DISCUSSION

Gomortegaceae, with $x = 21$, is evidently palaeohexaploid and this fact alone tends to suggest affinities with other families of the Magnoliales with a similar level of ploidy. Gomortegaceae is in fact most frequently allied with the so-called lauralian group of families, including Monimiaceae, Atherospermataceae, Siparunaceae, as well as Lauraceae, Hernandiaceae, and possibly Lactoridaceae. Of these, all but Lauraceae ($x = 12$) have high basic numbers, ranging from $x = 22$ in Atherospermataceae and Siparunaceae, $x = 19$, 18 (possibly also 22) in Monimiaceae (Goldblatt, 1974), $x = 20$ in Hernandiaceae, and $x = 20$ (or 21) in Lactoridaceae (Raven, 1975).

A relationship with Lauraceae and also with Canellaceae has been suggested for *Gomortega*. Studies of wood anatomy (Stern, 1955) and in the case of Canel-

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[1] Dr. F. Schlegel-Sachs, Universidad Austral de Chile, is gratefully thanked for his generous help in obtaining the seed and plants of *Gomortega* used in this study.

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laceae, pollen morphology (Erdtman, 1952), appear to refute any close relationship; this now seems to be supported by the cytological evidence, with both Lauraceae and Canellaceae palaeotetraploid.

Closer affinities with Monimiaceae, Atherospermataceae, and Siparunaceae, indicated by Stern (1955) and more recently by Schodde (1970) and Thorne (1974), seem more likely. *Gomortega*, with endospermous seeds (in contrast to the nonendospermous seeds in Lauraceae), does appear better placed among these families, particularly Atherospermataceae and Siparunaceae, both of which also have valvate anthers. Pollen morphology does not contradict this since nonaperturate grains like those found in *Gomortega* also occur in certain Monimiaceae and Siparunaceae (Erdtman, 1952). The base number of $x = 21$ in *Gomortega* certainly accords with the placement of this family among Atherospermataceae, Siparunaceae ($x = 22$), and Monimiaceae ($x = 19$). There is, however, some doubt that these latter three are themselves closely allied (Schodde, 1970), though Atherospermataceae and Siparunaceae may have had a common origin.

On balance it appears that Gomortegaceae is more closely related to this group of lauralian families than to others in the alliance and the cytological data strongly support Schodde's (1970) contention that Gomortegaceae is most closely allied to Atherospermaceae. Additional support for this is found in geographical considerations, with Atherospermataceae occurring in Chile as well as Australia. Other possible affinities cannot be excluded and further data on chromosomes, as well as other information about the fairly large and varied Monimiaceae, may yield valuable information concerning relationships among the families Gomortegaceae, Atherospermataceae, Siparunaceae, and Monimiaceae.

LITERATURE CITED

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. Chronica Botanica Co., Waltham, Massachusetts.

GOLDBLATT, P. 1974. A contribution to the knowledge of cytology in Magnoliales. J. Arnold Arbor. 55: 453–457.

RAVEN, P. H. 1975. The bases of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62: 724–764.

———, D. W. KYHOS & M. S. CAVE. 1971. Chromosome numbers and relationships in Annoniflorae. Taxon 20: 479–483.

SCHODDE, R. 1970. The new suprageneric taxa in the Monimiaceae alliance (Laurales). Taxon 19: 324–328.

STERN, W. L. 1955. Xylem anatomy and relationships of Gomortegaceae. Amer. J. Bot. 42: 874–885.

THORNE, R. F. 1974. A phylogenetic classification of the Annoniflorae. Aliso 8: 147–209.

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The Woody Plants of Alabama

This important publication by Ross C. Clark provides a rich source of information concerning the 437 species of woody plants known to occur in Alabama. Notes on each species include its scientific name, common name, flowering and fruiting season, and the kind of habitat in which it occurs. An individual map for each species plots its distribution in Alabama. Keys provide the primary means for identifying the families and species of plants. The introduction presents information on Alabama's soils, geology, and climate—important factors in determining what plants grow there.

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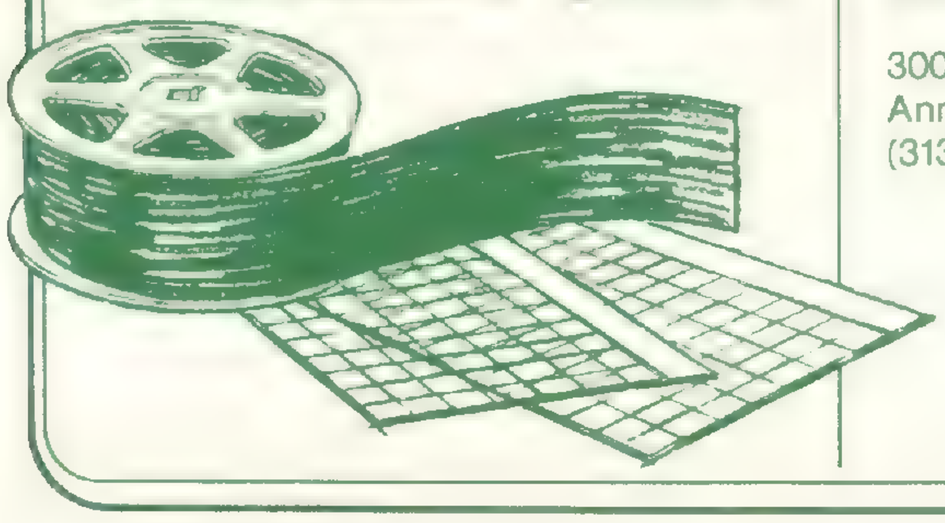

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ANNALS
OF THE
MISSOURI BOTANICAL GARDEN

VOLUME 63 1976 NUMBER 2

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EVOLUTION AT THE POPULATION LEVEL: THE TWENTY-SECOND SYSTEMATICS SYMPOSIUM

GERRIT DAVIDSE[1]

The following six papers were presented at the Twenty-second Annual Systematics Symposium held in the Lehmann Building of the Missouri Botanical Garden, 17–18 October 1974. Attended by nearly 300 scientists and graduate students, this yearly event brings together botanists and zoologists from throughout the United States to learn about and discuss recent developments in systematics and closely related fields. Expenses were in part borne by a National Science Foundation grant (GB-36049) and this support is gratefully acknowledged. Dr. Theodore Fleming, University of Missouri-St. Louis, served very capably as moderator, and Dr. Paul R. Ehrlich, Stanford University, presented a stimulating evening talk reviewing his research on the population biology of butterflies and more recently, coral reef fishes. It was presented under the title: "Butterflies, or the Truth Will Out." It is not published as part of this Symposium.

Since systematists and taxonomists classify evolutionary end-products and are intimately concerned with evolutionary processes, it was most fitting that some aspects of these processes could be considered at the population level in this Systematics Symposium. Dr. Hampton L. Carson spoke on adaptation and speciation at the microevolutionary level and attempted to identify the genetic basis for adaptational and speciational events. Dr. Janis Antonovics examined the nature of limits to natural selection based on his own and his students' studies of plant populations. Dr. George Johnson presented strong evidence for the natural selection of certain forms of enzymes that enable *Colias* butterflies to adapt more successfully to different montane environments. Dr. Otto T. Solbrig proffered a hypothesis to account for the development of the two main breeding systems in plants, cross- and self-fertilization. Dr. Robert W. Cruden discussed floral adaptations to insect pollination. Dr. José Sarukhán analyzed the markedly different life histories of three closely related species of buttercups and discussed possible types of selection that may be involved.

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THE UNIT OF GENETIC CHANGE IN ADAPTATION AND SPECIATION

HAMPTON L. CARSON[1]

ABSTRACT

Genetic variability in natural populations is very great. To a large degree, the types of variation found reflect the methods used. Thus we may recognize, segregating in natural populations, (1) point mutations (oligogenes) which have visible or physiological effects, (2) lethal and semilethal genes, (3) chromosome aberrations, and (4) soluble protein variability. This paper adduces cases which suggest that evolutionary change (adaptation or speciation or both) can occur without significant participation by any of the four classes of variation listed above. Thus, some cases of newly-formed species are known in which the species pair is chromosomally homosequential. Other cases show very little soluble protein (allozyme) difference (similarity coefficients of 0.95 or higher). These species appear to be much more newly formed than the classical "sibling" species of the *obscura* or *willistoni* groups of *Drosophila*. Nor does their biochemical similarity mean that such species differ by only a few genes. Rather, the genetic differences which characterize species when they are first formed may be numerous and largely of a regulatory nature. New recombinationally-synthesized blocks of epistatically interacting polygenes may also characterize newly-formed species. A theory that the amount of soluble protein change is primarily a function of time since the separation of two lineages is presented. This is apparently supported by allozyme data on eight species of *Drosophila* inhabiting Hawaiian islands of successively younger times of origin.

Ten years ago, systematic and evolutionary biology suddenly found itself wedded to molecular genetics. This strange affair came about because of the application of the new electrophoretic techniques to the genetic state of individuals in natural and artificial populations. The effect of this new biochemical genetics has been galvanic, especially in population genetics. Although traditionally strong in theory, this field had been struggling along for years with techniques of genetic analysis which could be applied to only a few kinds of organisms. Under the influence of these new techniques, however, both systematics and ecology have become deeply involved in a biochemical approach. Revolutionary ideas have been popping up on every hand. The purpose of the present discussion is to take a brief look back over the last few eventful years to see if major new concepts may be discerned.

ADAPTATION

How does the natural genetic variability within a species relate to the immediate needs of the organism? To what extent do the genes track the environment? First to be discovered were the recessive "visible" mutations which can be segregated out, from specimens collected in the wild, by inbreeding their progeny in the laboratory. Following this, variants which are manifested cytologically, like inversions and translocations, came to light. Many of these were shown to exist as balanced polymorphisms in nature. Still later, as genetic techniques became more sophisticated, precise methods revealed a further wealth

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of variability based on recessive lethal genes, which were also shown to be carried widely in natural populations. Then came renewed emphasis on polygenic variability, a source of variation which had been long exploited by the animal and plant breeder. There is no question that a large store of polygenic genetic variability also characterizes natural populations. Laboratory, population-cage and field-plot selection experiments have revealed the reality and ubiquity of these polygenic systems (for a recent review, see Mather, 1973).

Then Markert's ingenious and simple starch-gel techniques came to be applied to natural populations. This trend developed into a virtual orgy of biochemical research as allozyme and other soluble protein variation has been catalogued in populations of mice, horseshoe crabs, elephant seals, wild oats and, of course, many, many kinds of *Drosophila*. The majority of the loci that encode for soluble proteins show levels of polymorphism and individual heterozygosities which are almost universally high. The amount of data generated in the last few years boggles the mind.

Perhaps because biochemical data are glamorous or because the methods are so elegantly simple, soluble protein variability seems now to be considered consonant with, or at least representative of, genetic variability in the broad sense. Thus, in the current literature, "genetic variation" and "genetic similarity" are used as synonyms of "electrophoretic variability" (or similarity). By inference, the other types of genetic variability seem to have been assigned relatively minor roles and biochemical variation assigned a major one. In the flush of excitement over allozymes, it sometimes seems that the other types of genetic variability have been partially forgotten. The time seems right for a revival of interest in these other types of genetic variability.

The present article attempts a review of the relative importance of these various sorts of genetic variability with regard to the dynamic changes in populations that we call the evolutionary process. My general theme is that neither the soluble proteins nor the structural chromosome changes satisfy the requirements for the genetic variability which is related to adaptation. The most important variation seems to be that generated by recombination from the polygenic systems and the regulatory genes which control them.

The adaptive process takes place only at one point in nature; that is, within the local population, or deme. Furthermore, it can occur only in a population which maintains a genetically variable gene pool. Under natural selection, the genetic composition of the population shifts in response to environmental demands. As an intrademic process, occurring in time, such tracking of the environment is basically phylogenetic in the sense that the population passes as a whole from one genetic composition to another during passage of time. This type of change is sometimes referred to as anagenesis, as contrasted with cladogenesis, a process in which the population splits and then becomes genetically different in its different branches.

A number of natural and experimental instances of environmental tracking are well known. I refer to such cases as industrial melanism in moths, copper tolerance in plants, DDT resistance in insects, and antibiotic resistance in microorganisms. A recent striking case of copper resistance in *Paramecium* has been

described by Nyberg (1975). One may also cite the many accomplishments of the plant and animal breeders whose engineering is simply applied microevolution.

Whereas the reality of these changes at the genotypic level cannot be doubted, considerable question remains as to exactly what kind of genetic alteration occurs as the population responds. In a number of instances, of course, the frequencies of specifically recognizable genes are changed; certain alleles may, in fact, become fixed. This result has been taken as a basic model of evolutionary change. In 1957, Haldane wrote: "The principal unit process in evolution is the substitution of one gene for another at the same locus."

On the other hand, significant genetic change under selection can occur with only minor change in gene, inversion, lethal, or allozyme frequency. The result cannot always be described as simply as Haldane's dictum suggests. Rather, selection appears to be favoring a new balanced combination of genes, an interacting and flexible unit. Kenneth Mather, a leading proponent of this theory for 30 years, long ago (1943) invoked the idea of both internal and relational balance. Through recombination at meiosis and syngamy, the genetic architecture of an organism usually rests at an equilibrium determined by opposing selective forces. When a new directional selective force is applied, effects are manifold throughout the genotypic system. Genetic recombination is viewed as a force which generates new gene combinations, always tending to perturb the status quo. A novel selective force may favor some of the products of this perturbation, causing the balance to shift to a new equilibrium. Simple substitution at a locus is seen only rarely.

The theory of coadaptation of genes, advanced by Dobzhansky, Wallace, and others as an explanation for balanced polymorphisms, bears considerable similarity to the balance theories of Mather. Thus shifting polymorphisms involving inversions, visibles, or allozymic loci in natural or experimental populations may all be viewed as changes which reflect shifts in gene interaction. Attention in these theories moves away from the single locus reacting in isolation. On the other hand, it emphasizes the shift in balance within the system. Even if not explicitly stated, shifting balance theory underlies much of the data of evolutionary genetics.

Considerations of this sort, furthermore, render the now waning "neutralist vs. selectionist" controversy somewhat meaningless. The views of both protagonists appear to oversimplify by treating the single gene as the unit of anagenetic evolutionary change.

On the other hand, Franklin & Lewontin (1970) and Lewontin (1974) have discussed what they call the "unit of selection." They suggest that in many, if not most, cases selection cannot be so simple as to favor a single-locus zygotic state, as if it were isolated in a neutral background. If there is value in such a view, it means that selection may indeed force a gene frequency change at an electrophoretically-detected locus, for example, without directly favoring or disfavoring the immediate gene product of that locus (e.g., see Stam, 1975). Changes in gene frequency may thus be correlated because it is the interacting system as a whole which is the unit of selection. Linkage is a powerful genetic force and may

be invoked, as Mather has done, to explain the many synergistic effects elsewhere in the organism when selection is artificially placed on a single character such as sterno-pleural bristle number in *Drosophila* (see the classic paper of Mather & Harrison, 1949).

Linkage disequilibrium, which is a manifestation of strong organizational forces operating on the balances and interactions of genes, has, in fact, been rather widely reported. Numerous cases are known, for example, where two or more linked inversions are held out of equilibrium by what are apparently strong selective forces (see Levitan, 1958, for review); striking cases are reported by Stalker (1960, 1964) and Sperlich & Feuerbach-Mravlag (1974). Perhaps it should be stressed that these cases are of disequilibrium *between* inversions. The inversion itself, of course, has well-known properties which lead to association of genes within it into a supergene (see Dobzhansky, 1959). This is indeed association, but it is not quite the same as the case when two or more inversions in the same chromosome show linkage disequilibrium. It is possible that the latter reflects a major organization of the genetic system rather than a property peculiar to simple recombination-blockage by an inversion.

Disequilibria in the absence of inversions are particularly crucial, in that they reveal associations which are maintained in the absence of any of the widely-recognized bars to crossing-over. Very clear cases have been adduced by Cannon (1963), Zouros & Krimbas (1973), Sinnock & Sing (1972), Charlesworth & Charlesworth (1973), and Roberts & Baker (1973). Mukai et al. (1974) have shown disequilibria between certain isozyme loci and adjacent inversions. Jones & Yamazaki (1974) have shown that linkage disequilibrium can affect allozyme frequencies in an experimental situation. In view of the technical difficulties attendant on the recognition of such systems these cases seem quite numerous. The theoretical work on the dynamic aspects of such systems (e.g., Lewontin & Kojima, 1960; Franklin & Lewontin, 1970) stresses that the situation may be very complex, even if only two loci are involved. Indeed, the evidence usually cannot exclude the operation of multilocus systems of very great complexity.

These remarks may bring to mind the polemics of Goldschmidt (1940), some 35 years ago. We need not, however, embrace the "chromosome as a whole" and reject the gene concept to invoke the existence of balanced blocks of interacting genes. I am fully aware that it is easy to play a somewhat pontifical role in this field, accusing the mathematically-inclined of oversimplification and advancing as a substitute theories of "shifting balance." I do it not in an effort to denigrate the work of others but rather in an attempt to stimulate study of these more complex and subtile phenomena by those who possess the practical tools and theoretical orientation to do so.

In the last few years, several situations have come to light which suggest a new approach to a more realistic unit of selection (or unit of random drift, for that matter). For example, Carson (1967, 1973) and Carson et al. (1969) have shown that, under selection, some strains of the normally bisexual species *Drosophila mercatorum* will give rise to vigorous and self-sustaining laboratory stocks which reproduce wholly without males. By rather simple genetic methods, it was shown that not only are the females which comprise such a stock diploid but

also that the stock acquires a completely isogenic state. How can the genotype of a normal bisexual species become so readjusted as to permit its carriers to survive and reproduce despite the vigors imposed by a complete and total homozygosity? Sing & Templeton (1975), and Templeton et al. (1976a, 1976b) have provided evidence that the capacity of these strains to reproduce in this manner is based on a multilocus genetic organization or coadaptation of genes which permits such total homozygosity. Development and reproduction are impaired if this coadaptation is perturbed by recombination away from a particular internally balanced state. Selection back to the original coadapted state occurs largely at the zygotic stage. Perturbation of even small sections of the genome give evidence of the existence of a true coadaptation involving nonadditive interactions between nonalleles. The capacity for parthenogenesis in these stocks, therefore, is related to a complex genetic organization of genes of individually minor or insignificant effects.

The importance of the Sing and Templeton work, which is just beginning, is that it provides a new technique for analyzing the unit of selection with great sensitivity. The model they have adduced would appear to have wide application to the understanding of gene interaction in all kinds of diploid systems. The parthenogenetic system that they have used merely provides an elegant tool for the stabilization and then dissection of the underlying genetic state.

In considering the genetic basis for adaptive change in populations, these balance theories have another important implication. The entire genome of the species is not under obligation to mount a response to selective pressure from the external environment. Goodhart (1963), Clarke & Murray (1971) and Jones (1973) have urged that greater attention be given to "area effects" wherein certain local areas show unique and persistent epistatic relationships between genes. Thus local climatic selection may find itself working on a genetic environment which is, because of epistatic balance, somewhat refractory to a quick and simple genetic response. In a recent paper (Carson, 1975) I have suggested that some of the assumed relationally balanced polygenic blocks in a species may become essentially fixed species-characteristics which are closed to recombination because of the inviability or biological inefficiency of the crossover products. The prevailing view that the thousands of loci along a chromosome are all available in any combination seems to me simplistic and not in accord with the data surrounding the various kinds of natural and artificial selection.

To what extent is the allozymic variation carried within a species relevant to the type of adaptational adjustments just discussed? This complex question may be approached by comparing local populations within a species to see how closely such variation tracks the ecological diversity within the species range. Indeed, direct correspondence appears to be very low. Many species show a remarkable genetic similarity between their local geographical populations despite wide differences in geography and ecology (Prakash et al., 1969; Prakash, 1973; Ayala et al., 1972). Both Mukai et al. (1974) and Zouros (1975) have questioned whether allozymic variation is maintained by balancing selection.

In these studies and similar ones, a very useful method of data-reduction has been employed, namely, the indices of genetic similarity (or distance) between

pairs of populations (e.g., Nei, 1972; Rogers, 1972). When compared, local populations of the same species tend to show a similarity index of 0.95 or above (1.0 would indicate identity). This very remarkable similarity between such populations suggests that the allozymic variability does not form the basis for a simple and direct relationship between microadaptation and allozymic loci. In artificial populations of *D. willistoni*, Powell (1973) observed frequency changes in alleles at allozyme loci, but he is careful to point out that these changes might be due to the association of these loci with larger gene blocks, such as inversions. Accordingly, the old problem as to what is the unit of selection again appears.

In a similar manner, it is difficult to associate inversion variability with specific microadaptational response. Inversions, unlike most allozyme polymorphisms, frequently show geographical clines and artificial selection sometimes elicits a response from these chromosome variants. On the other hand, as has been argued by Dobzhansky and others, it appears to be coadaptive gene balances which change geographically. After all, inversions are gene blocks. When they undergo significant frequency changes with altitude, temperature or other environmental parameters, hundreds of gene loci are undoubtedly involved in the geographical shift.

Inversions, furthermore, are dispensable in microevolution. Among 95 Hawaiian picture-winged *Drosophila* species assayed for inversion variability, 65 (68%) show no intraspecific inversions whatsoever (Clayton et al., 1972). Indeed, this shows that adaptive microevolution does not require segregating cytological variation, because only one-third of the species studied exploit the advantages of inversions, whatever these advantages are.

In cases of species where both allozymic and chromosomal variability is present, local populations appear to show more differentiation in chromosomes than in allozymes (Prakash, 1973; Carson et al., 1975). This may be because the inversion, on the average, can embrace and thus mark a larger "chunk" of the genome than the allozyme locus.

In conclusion, selection appears to effect a genetic response by favoring various balanced combinations of genes. Single loci are rarely favored *per se* but mainly as part of an interacting group of genes. Not all of the genetic material of the species is open to the recombinational system which generates the balances that selection operates on. Inversions are dispensable to the functioning of the process but, when present, they form an efficient means for developing and holding epistatically balanced gene blocks.

Speciation

This process contrasts with anagenesis in that a branching, or cladistic, event is involved. What was formerly a single population splits into two and these subsequently come to be recognized as different biological species. Unlike anagenesis, cladogenesis has been rather refractory to analysis.

Part of the difficulty lies in interpreting the time of origin of the genetic differences displayed by the two species. Some, if not most, of the differences that we observe have undoubtedly been added after the cladistic event has taken place and, accordingly, are not relevent. If we could recognize this category of

differences and subtract them, we would be left with the crucial syndrome of differences which arose synchronously with the cladogenetic events. This might lead to a simplification of the problem; an attempt in this direction will be adduced later in this section.

For reasons set forth in several recent publications (Carson, 1970, 1971, 1975) I have questioned whether speciation is universally the outcome of a direct response to an environmental need. Have the genetic changes which accompany speciation been established under selective control and in the same manner as discussed above for adaptation? These considerations are based on observations drawn from various exhuberantly speciated insular biotas. These facts suggest that species-splitting is consequent on a sudden strong geographical isolating event such as occurs when a daughter population is founded, allopatrically to the progenitor population, from one or very few individuals.

Under these circumstances, speciation may have a strong stochastic element. The new isolated population is forced, perhaps because of the attenuation and disruption of the old gene pool at the founder event, to evolve a new system of internal genetic balances. Incipient reproductive isolation could be initiated as a chance accompaniment of this process. This forced reorganization of the genome may be initially established by selection for a new kind of genetic balance rather than representing any tracking of external environment. The latter, as well as the completion of isolation, would be expected to follow, rather than be synchronous with, the cladistic event.

In discussing reorganization in anagenesis, mention was made of the many such changes observed by Templeton et al. (1976a, 1976b) as parthenogenetic strains are formed. Similar genetic revolutions (see Mayr, 1954, and Carson, 1975) may indeed be important as an early stage of speciation. Lewis & Raven (1958) and Gottleib (1974) have stressed the element of chance in certain plant speciation patterns.

A more traditional view of geographic speciation calls for the gradual formation of species through a geographical subspecies as an intermediate stage. This occurs because allopatric populations of the same species may become genetically differentiated as a consequence of their adaptation to different environments. A second stage of the process calls for selection which favors reproductive isolation between the two genetically differentiated populations. Subspecies which have acquired incomplete biological isolating mechanisms are sometimes referred to as semispecies. Only when reproductive isolation is complete can full specific status be assumed.

As a paradigm of this gradual speciation process, Ayala et al. (1974) have adduced the case of the *willistoni* group of *Drosophila*. They recognize five increasingly divergent levels of cladogenesis. These may be observed by comparisons (1) between geographic populations within a species, (2) between subspecies, (3) between semispecies, (4) between sibling species, and (5) between morphologically distinguishable species of the same group. These authors have suggested that the allozymic genetic differences accumulate gradually over these levels of divergence. Thus, whereas local populations show allozyme similarity indices of about 0.97, subspecies and semispecies average 0.8 similarity when

examined by pairs. Sibling species show a similarity of about 0.5 and nonsibling species about 0.35. These indices are based on allozymes alone; other kinds of genetic differences are not taken into account. In the *willistoni* group, semispecies seem not to differ in their allozymic similarities from subspecies. Ayala et al. interpret this to mean that the initial isolations depend on a rather small number of genes.

Although the above scheme seems to fit the *willistoni* group rather well, it appears not to fit certain other *Drosophila* situations, notably the Hawaiian *Drosophila*. Johnson et al. (1975), for example, have calculated similarity coefficients based on allozymes for sixteen species of the *planitibia* subgroup. Two of them (*D. heteroneura* and *D. silvestris*) are endemic to the geologically very recent Island of Hawaii. These two new species are strikingly different in color and morphology and coexist sympatrically. They show an allozymic similarity coefficient of 0.96, similar to the level shown for intraspecific local populations of the members of the *willistoni* group. Such very high allozyme similarities are also found between some other pairs of species of the *planitibia* subgroup on the Island of Maui (Johnson et al., 1975). A similar situation obtains for another pair of sympatric species, of a different subgroup, for Hawaii Island (Carson et al., 1975). In both of these cases, morphology and chromosomal characters are more efficient in differentiating species than are the electrophoretic differences.

Soluble protein (allozymic) differences have been shown to be minimal between species in a number of other cases. Thus, Turner (1974) found minimal divergence among five species of pupfish from the Western United States; Koehn (1967) obtained similar results. Avise (1975) reports that several species-pairs of *Peromyscus* show similarity coefficients above 0.95 and Avise et al. (1975) find that the same is true of two California minnows (*Hesperoleucus symmetricus* and *Lavinia exilicauda*). These have been referred by systematists to different genera! King & Wilson (1975) have assembled a large amount of data which show that man and chimpanzee, likewise assigned to different genera, are as similar to one another biochemically as a pair of sibling species of *Drosophila*. Certain plants show a similar pattern. Thus Gottleib (1973, 1974) has found very close allozymic similarities between species-pairs in *Clarkia* and in *Stephanomeria*.

Accordingly, it appears that in a number of cases speciation can occur without significant alteration in genetically-determined soluble proteins. It is also well documented in the data on Hawaiian *Drosophila* that many closely related species are homosequential in all of the polytene chromosomes (see Clayton et al., 1972), indicating that speciation can indeed occur without sequential alteration or indeed any participation by inversions or translocations in the process. Even genes which determine external morphology may remain basically unchanged as in the well-studied cases of sibling or morphologically cryptic species in many sections of the genus *Drosophila*.

Thus, to sum up the present argument, crucial cases exist showing that speciation in diploids can proceed without significant alteration in structural chromosome sequence, soluble proteins, or the genetic basis of external morphology. Differential adaptation is not a prerequisite. This brings us again to the concept

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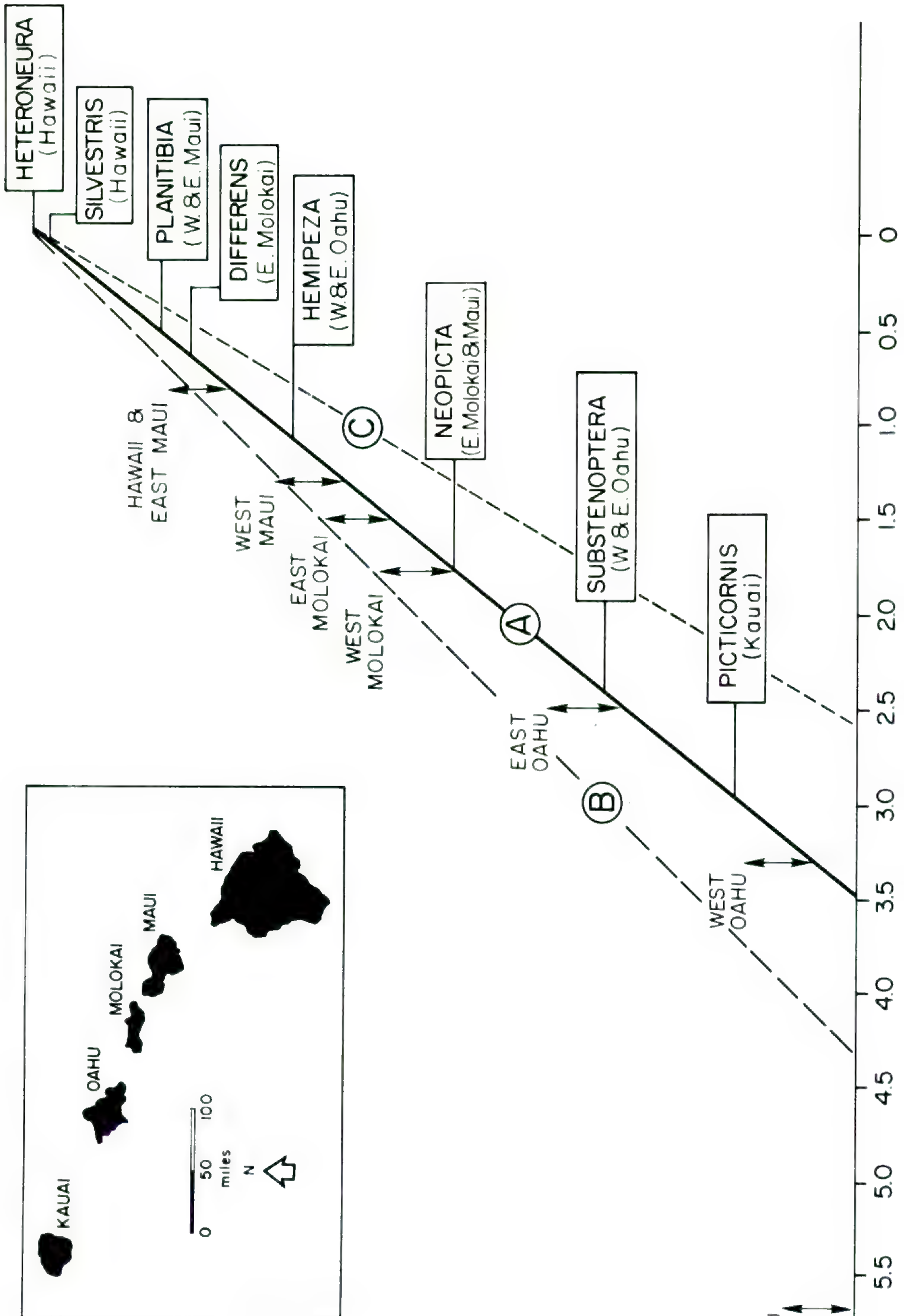
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SILVESTRIS (Hawaii)
PLANITIBIA (W.&E. Maui)
DIFFERENS (E. Molokai)
HEMIPEZA (W.&E. Oahu)
NEOPICTA (E. Molokai & Maui)
SUBSTENOPTERA (W. & E. Oahu)
PICTICORNIS (Kauai)
HAWAII & EAST MAUI
WEST MAUI
EAST MOLOKAI
WEST MOLOKAI
EAST OAHU
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TIME BEFORE THE PRESENT (millions of years)
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ALLOZYMIC DIFFERENCE FROM HETERONEURA (−log$_e$ S)

of polygenic balance, which was discussed earlier, and to the subject of gene regulation. The latter concept has been recently invoked to explain important evolutionary changes. Wilson et al. (1974), for example, ". . . regard adaptive evolution as resulting primarily from changes in the expression of genes relative to one another rather than from amino-acid substitutions in the products of those genes."

Direct knowledge of gene regulation in eukaryotic systems is exceedingly rudimentary. Extrapolation from the elegant systems which are known in prokaryotes are widely made but should be viewed with caution. This will not be the first time, however, that evolutionary genetics has been forced to consider developmental control of the phenotypes on which the evolutionary process operates.

Electrophoretic Data as an Evolutionary Clock

Much attention has been given in recent years to the interpretation of protein evolution through amino-acid substitution (e.g., Fitch, 1972; Langley & Fitch, 1974). At the level of the species population, furthermore, strong arguments have been advanced that the allozymic variation is neutral or quasi-neutral to selection (for a recent formulation, see Ohta & Kimura, 1975; see also Zouros, 1975). Accordingly, there may also be a direct correlation between high allozymic similarity and the recency of the cladistic event which separated the two compared entities.

A line of evidence suggesting such a passive role for allozymic differences in evolution is provided by some data cited by Avise & Ayala (1975, 1976). The North American minnows (family Cyprinidae) are highly species-rich. Since the late Miocene, some 250 species have been formed. Although evolving over similar geologic time, the sunfish genus *Lepomis* is species-poor, having produced a total of only 11 species. Differential extinction rates in the two phylads can apparently be ruled out. Avise and Ayala ask whether the mean allozymic difference between existing species is related to the number of cladistic events in the phylad or whether it is a function of time since the first cladistic event. The coefficients are remarkably similar when the products of the species-rich and species-poor phylads are compared. The authors conclude that time since divergence from a common ancestor is more important than the number of intermediate cladistic events in determining the level of allozymic divergence between species.

If decay of similarity is progressive and related to the length of time since the

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Figure 1. Allozymic difference and time of species origin in eight species of Hawaiian *Drosophila* (*planitibia* subgroup). Allozyme differences (pairwise comparisons with *D. heteroneura*) are plotted against the age of the oldest recorded rocks of each island or volcano. Under each species name is indicated the island (or volcano) to which that species is endemic. Diagonal line *A* assumes a uniform accumulation of difference of 1% each 20,000 years. From this, the time of each past species origin is predicted. Diagonal *B* represents a slower rate of change (1% difference in 25,000 years). Diagonal *C* assumes faster change (1% difference in 15,000 years). Diagonal *A* gives the most satisfactory fit to the geological and geographical data.

ancestral splitting, allozymic differences might be used in some circumstances as a clock to determine evolutionary rates and, indeed, the time of past cladistic events. An example may be taken from certain *Drosophila* species of the Hawaiian Islands (Carson, 1976). The ages of five of the largest and most southeasterly Hawaiian islands are accurately known from magnetic declination and potassium-argon data (Macdonald & Abbott, 1970). One of the two sympatric species of the *Drosophila planitibia* subgroup endemic to the geologically most recent Island of Hawaii (*D. heteroneura*) may be compared by pairs with seven of its close relatives for allozyme similarity (S values of Rogers; see Johnson et al., 1975). Assuming that allozymic genetic difference accumulates at a uniform rate, the coefficients of genetic difference ($D = -\log_e S$) of these seven from *heteroneura* may be plotted against time as indicated by the age of the islands to which these flies are endemic (Fig. 1).

An assumed rate of accumulation of genetic difference of 1% in 20,000 years fits the ages of the islands and the inferred times of cladogenesis rather well. Faster or slower differentiation (i.e., 1% in 15,000 or 1% in 25,000 years) produces a less satisfactory fit of the data to the geological and biological facts (Fig. 1). These observations are in line with the idea, stated earlier in this paper, that speciation has an initial stochastic element. Thus, the Hawaiian *Drosophila* of the Island of Hawaii, the pupfish of Death Valley, the cyprinid minnows of California, and *Clarkia biloba* and *C. lingulata* may all be examples of recent speciation. They may have not had enough time to accumulate much allozymic difference. According to this view, the members of the continentally distributed *willistoni* group of *Drosophila* species diverged from one another in the much more distant past so that allozymic differentiation between some subspecies, for example, is greater than that between species in the other very newly formed taxa mentioned above.

CONCLUSION

Numerous cases exist wherein both speciation and adaptation can proceed in the absence of genetic fixation involving allozymes, chromosomal aberrations, heterochromatin differences, "visible" genes, lethals and morphological differences. If no one of these various known types of genetic variation is an absolute requirement, it follows that we must look elsewhere for an underlying common genetic element. The suggestion is made in this paper that evolution has, as its common denominator, a shifting internal balance of gene interactions in which a strong role is played by regulatory genes. Such a formulation can be invoked to explain the stochastic nature of some speciations following founder events. Although allozymic variation may be trivial with regard to selection, it may turn out to be useful as a clock from which we may read the age of a species.

LITERATURE CITED

AVISE, J. C. 1975. Systematic value of electrophoretic data. Syst. Zool. 23: 465–481.
——— & F. J. AYALA. 1976. Genetic differentiation in speciose versus depauperate phylads: Evidence from the California minnows. Evolution 30: 46–58.
——— & ———. 1975. Genetic change and rates of cladogenesis. Genetics 81: 757–773.

———, J. J. Smith & F. J. Ayala. 1975. Adaptive differentiation with little genic change between two native California minnows. Evolution 29: 411–426.

Ayala, F. J., J. R. Powell, M. L. Tracey, C. A. Mourão & S. Pérez-Salas. 1972. Enzyme variability in the *Drosophila willistoni* group. IV. Genic variation in natural populations of *Drosophila willistoni*. Genetics 70: 113–139.

———, M. L. Tracey, D. Hedgecock & R. C. Richmond. 1974. Genetic differentiation during the speciation process in *Drosophila*. Evolution 28: 576–592.

Cannon, G. B. 1963. The effects of natural selection on linkage disequilibrium and relative fitness in experimental populations of *D. melanogaster*. Genetics 48: 1201–1216.

Carson, H. L. 1967. Selection for parthenogenesis in *Drosophila mercatorum*. Genetics 55: 157–171.

———. 1970. Chromosome tracers of the origin of species. Science 168: 1414–1418.

———. 1971. Speciation and the founder principle. University of Missouri Stadler Symposia 3: 51–70.

———. 1973. The genetic system in parthenogenetic strains of *Drosophila mercatorum*. Proc. Natl. Acad. U.S.A. 70: 1772–1774.

———. 1975. The genetics of speciation at the diploid level. Amer. Naturalist 109: 83–92.

Carson, H. L. 1976. Inference of the time of origin of some *Drosophila* species. Nature 259: 395–396.

———, I. Y. Wei & J. A. Niederkorn, Jr. 1969. Isogenicity in parthenogenetic strains of *Drosophila mercatorum*. Genetics 63: 619–628.

———, W. E. Johnson, P. S. Nair & F. M. Sene. 1975. Allozymic and chromosomal similarity in two *Drosophila* species. Proc. Natl. Acad. U.S.A. 72: 4521–4525.

Charlesworth, B. & D. Charlesworth. 1973. A study of linkage disequilibrium in populations of *Drosophila melanogaster*. Genetics 73: 351–359.

Clarke, B. & J. Murray. 1971. Polymorphism in a Polynesian land snail *Partula suturalis vexillum*. Pp. 51–64, *in* R. Creed (editor), Ecological Genetics and Evolution. Blackwell Publ., Oxford.

Clayton, F. C., H. L. Carson & J. E. Sato. 1972. Polytene chromosome relationships in Hawaiian species of *Drosophila*. VI. Supplementary data on metaphases and gene sequences. Univ. Texas Publ. 7312: 163–177.

Dobzhansky, T. 1959. Evolution of genes and genes in evolution. Cold Spring Harbor Symp. Quant. Biol. 24: 15–30.

Fitch, W. M. 1972. Does the fixation of neutral mutations form a significant part of the observed evolution in proteins? *In* H. H. Smith (editor), Evolution of Genetic Systems. Brookhaven Symp. Biol. Vol. 23: 186–216.

Franklin, I. & R. C. Lewontin. 1970. Is the gene the unit of selection? Genetics 65: 707–734.

Goldschmidt, R. 1940. The Material Basis of Evolution. Yale University Press, New Haven. 436 pp.

Goodhart, C. B. 1963. "Area Effects" and non-adaptive variation between populations of *Cepea* (Mollusca). Heredity 18: 459–465.

Gottleib, L. D. 1973. Genetic differentiation, sympatric speciation and the origin of a diploid species in *Stephanomeria*. Amer. J. Bot. 60: 545–554.

———. 1974. Genetic confirmation of the origin of *Clarkia lingulata*. Evolution 28: 244–250.

Haldane, J. B. S. 1957. The cost of natural selection. J. Genet. 55: 511–524.

Johnson, W. E., H. L. Carson, K. Y. Kaneshiro, W. W. M. Steiner & M. M. Cooper. 1975. Genetic variation in Hawaiian *Drosophila*. II. Allozymic differentiation in the *D. planitibia* subgroup. *In* C. L. Markert (editor), Isozymes. Vol. 4. Genetics and Evolution. Academic Press, Inc., New York. pp. 563–584.

Jones, J. S. 1973. Ecological genetics and natural selection in molluscs. Science 182: 546–552.

——— & T. Yamazaki. 1974. Genetic background and the fitness of allozymes. Genetics 78: 1185–1189.

King, M. & A. C. Wilson. 1975. Evolution at two levels in humans and chimpanzees. Science 188: 107–116.

Koehn, R. K. 1967. Blood proteins in natural populations of catostomid fishes of Western North America. Ph.D. dissertation, Arizona State Univ., Tempe. 153 pp.

LANGLEY, C. H. & W. M. FITCH. 1974. An examination of the constancy of the rate of molecular evolution. J. Molec. Evol. 3: 161–177.

LEVITAN, M. 1958. Non-random associations of inversions. Cold Spring Harbor Symp. Quant. Biol. 23: 251–268.

LEWIS, H. & P. H. RAVEN. 1958. Rapid speciation in *Clarkia*. Evolution 12: 219–336.

LEWONTIN, R. C. 1974. The Genetic Basis of Evolutionary Change. Columbia Univ. Press, New York. 346 pp.

——— & K. KOJIMA. 1960. The evolutionary dynamics of complex polymorphisms. Evolution 14: 458–472.

MACDONALD, G. A. & A. T. ABBOTT. 1970. Volcanoes in the Sea. University of Hawaii Press, Honolulu. 441 pp.

MATHER, K. 1943. Polygenic inheritance and natural selection. Biol. Rev. Cambridge Philos. Soc. 18: 32–64.

———. 1973. Genetical Structure of Populations. Chapman and Hall, London. 197 pp.

——— & B. J. HARRISON. 1949. The manifold effect of selection. Heredity 3: 1–52.

MAYR, E. 1954. Change of genetic environment and evolution. Pp. 157–180, *in* J. Huxley (editor), Evolution as a Process. Allen and Unwin, London.

MUKAI, T., T. K. WATANABE & O. YAMAGUCHI. 1974. The genetic structure of natural populations of *Drosophila melanogaster*. XII. Linkage disequilibrium in a large local population. Genetics 77: 771–793.

NEI, M. 1972. Genetic distance between populations. Amer. Naturalist 106: 283–292.

NYBERG, D. 1975. Genetic analysis of copper resistance in *Paramecium aurelia* syngen. 4. Genetics 80: 463–473.

OHTA, T. & M. KIMURA. 1975. Theoretical analysis of electrophoretically detectable polymorphisms: models of very slightly deleterious mutations. Amer. Naturalist 109: 137–145.

POWELL, J. R. 1973. Apparent selection of enzyme alleles in laboratory populations of *Drosophila*. Genetics 75: 557–570.

PRAKASH, S. 1973. Patterns of gene variation in central and marginal populations of *Drosophila robusta*. Genetics 75: 347–369.

———, R. C. LEWONTIN & J. L. HUBBY. 1969. A molecular approach to the study of genic heterozygosity in natural populations. IV. Patterns of genic variation in central, marginal and isolated populations of *Drosophila pseudoobscura*. Genetics 61: 841–858.

ROBERTS, R. M. & W. K. BAKER. 1973. Frequency distribution and linkage disequilibrium of active and null esterase isozymes in natural populations of *Drosophila montana*. Amer. Naturalist 107: 709–726.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Publ. 7213: 145–153.

SING, C. F. & A. R. TEMPLETON. 1975. A search for the genetic unit of selection. *In* C. L. Markert (editor), Isozymes 4. Genetics and Evolution. Academic Press, New York. Pp. 115–129.

SINNOCK, P. & C. F. SING. 1972. Analysis of multilocus genetic systems in Tecumseh, Michigan. II. Consideration of the correlation between nonalleles in gametes. Amer. J. Hum. Genet. 24: 393–415.

SPERLICH, D. & H. FEUERBACH-MRAVLAG. 1974. Epistatic gene interaction, crossing over, and linked and unlinked inversions in *Drosophila subobscura*. Evolution 28: 67–75.

STALKER, H. D. 1960. Chromosomal polymorphism in *Drosophila paramelanica* Patterson. Genetics 45: 95–114.

———. 1964. Chromosomal polymorphism in *Drosophila euronotus*. Genetics 49: 669–687.

STAM, P. 1975. Linkage disequilibrium causing selection at a neutral locus in pooled *Tribolium* populations. Heredity 34: 29–38.

TEMPLETON, A. R., C. F. SING & B. BROKAW. 1976a. The unit of selection in *Drosophila mercatorum*. I. The interaction of selection and meiosis in parthenogenetic strains. Genetics. 82: 349–376.

———, H. L. CARSON & C. F. SING. 1976b. The population genetics of parthenogenetic strains of *Drosophila mercatorum*. II. The capacity for parthenogenesis in a natural, bisexual population. Genetics 82: 527–542.

TURNER, B. J. 1974. Genetic divergence of Death Valley pupfish species: biochemical versus morphological evidence. Evolution 28: 281–294.

WALLACE, B. 1953. On coadaptation in *Drosophila*. Amer. Naturalist 87: 343–358.

Wilson, A. C., V. M. Sarich & L. R. Maxon. 1974. The importance of gene rearrangement in evolution: evidence from studies on rates of chromosomal, protein and anatomical evolution. Proc. Natl. Acad. U.S.A. 71: 3028–3030.

Zouros, E. 1975. Electrophoretic variation in allelozymes related to function or structure? Nature 254: 446–448.

——— & C. B. Krimbas. 1973. Evidence for linkage disequilibrium maintained by selection in two natural populations of *Drosophila subobscura*. Genetics 73: 659–674.

THE NATURE OF LIMITS TO NATURAL SELECTION[1]

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ABSTRACT

Insufficient genetic variability and the swamping effects of gene flow are inadequate explanations of limits to natural selection. Comparison of evolutionary responses in different populations subjected to similar selective forces, comparison of rare and widespread species, and comparison of marginal and central populations are all neglected research areas that bear on the nature of limits to natural selection. Plant populations provide us with well-defined, operationally viable systems for addressing these comparisons. Several possible constraints on range extension of ecologically marginal populations are considered in detail. Selection on fitness components that are themselves negatively correlated will be ineffective: such negative correlations are to be expected in natural populations. Small size of marginal populations will reduce severely the probability of obtaining appropriate character combinations; it will increase the swamping effects of gene flow; and it may lead to inbreeding depression effects. Gene flow will have different effects depending on whether the genes concerned are effectively neutral, advantageous, or deleterious in the population into which they migrate. Gene flow will spread beneficial genes rapidly, but may retard divergence if density of marginal populations is low and swamping effects are high. Finally a population entering a new habitat is likely to meet new competitors and predators: the coevolutionary responses of the latter may counteract adaptive responses by the species undergoing range extension. All these factors are likely to interact in important ways in marginal populations. The study of limits to natural selection is likely to be a fruitful future research area, and one in which the detailed documentation of the systematist will provide invaluable baseline information.

"The species border is one of the most interesting phenomena of evolution and ecology, yet as a scientific problem it has been almost totally ignored."

"The essential stability of the species border would seem to contradict our belief in the power of natural selection. One would expect the species range to grow by a process of annual accretion like the rings of a tree. That this does not happen is particularly astonishing in the frequent cases where conditions beyond the borderline differ only slightly and in degree from conditions inside the species border."

E. Mayr (1963, Chapter 17)

Population genetics is today in a state of dissatisfaction and ennui. This crisis has come about from what is considered to be one of the most important technological breakthroughs the subject has ever experienced, namely, the use of electrophoresis to study variation at the enzyme level and, by inference, at the level of the gene. The result of this technique has been the discovery of a large amount of genetic variability in natural populations. Yet the cause of such a high level of genetic polymorphism has not been satisfactorily explained. The critical question is not so much can we determine which mechanisms predominate (and

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numerous mechanisms have now been proposed), but can we even distinguish operationally whether selection is acting at all on any particular locus. Given that we can identify genetic variation at a locus, can we pinpoint its phenotypic effect, can we establish its effect on fitness in nature, and, more crucially, can we say the effect is due to that locus and not closely linked genes? Given that the proportional contribution of any individual gene to fitness is likely to be low, these questions become formidable. It is salutary to note that there is still tremendous controversy regarding the mechanisms maintaining some phenotypically overt polymorphisms such as banding color and pattern in the land snail, *Cepaea* (e.g., Greenwood, 1974; Bantock, 1974; Clarke, 1975).

In order to escape from this crisis, either fresh questions need to be asked, or we need to take a fresh approach to old problems. In this paper I want to ask perhaps an obvious yet rarely considered question, namely, what limits natural selection, and pinpoint some approaches to answering it. I say the question is rarely considered, but strictly speaking this is not true, since in fact the question has been frequently asked; yet it has usually had a simple, almost tautological answer, namely, "lack of genetic variability" and the subject has thereby been closed. We now know this answer to be false at least at a superficial level.

Almost every species that has been studied is genetically variable at about 30% of its loci. We know that species which have remained unchanged, as far as we can judge, for millions of years still contain a tremendous amount of variability. The horseshoe crab, *Limulus polyphemus*, has been shown to be polymorphic at 25% of its loci, yet it is a "living fossil" whose close relatives date back 300 million years (Selander et al., 1970). Similarly, *Lycopodium lucidulum*, a clubmoss, has been shown to be polymorphic at 28% of its loci (when summed over all populations), and yet it is considered to be the most primitive living member of the lycopods which had their origin in the Devonian, ca. 400 million years ago (Levin & Crepet, 1973). And studies of rare or vanishing species have shown that these too are genetically variable. For example, the Orang Utan has been declining in abundance over thousands of years and is now a highly restricted species, yet it is one of the most polymorphic primates known (Buettner-Janusch, 1973, personal communication). Babbel & Selander (1974) have shown that the same number of loci were polymorphic in the edaphically restricted *Lupinus subcarnosus* as in the more widespread *Lupinus texensis*. The number of alleles per locus was greater in the more widespread species, but it was difficult to decide whether this was a cause or effect of its broader geographical range.

Other lines of evidence argue strongly not just for a high level of variation at the enzyme level, but also for a high degree of genetic variation in characteristics at the phenotypic level. The most powerful evidence for this comes from artificial selection experiments. For example, Antonovics (1975) and Lewontin (1974: 89) have collated lists of characters which have responded to artificial selection in *Drosophila melanogaster*: the lists are not exhaustive, yet the number of relatively independent traits that respond to selection is near 50. And Falconer (1960: 343) in summarizing what is known about quantitative variation, stated:

"The genetic variation of metric characters appears from the results of experimental selection to be the product of segregation at some hundreds of loci, or more probably some thousands if the variation of all characters is included. So natural populations probably carry a variety of alleles at a considerable proportion of loci, even perhaps at virtually every locus."

With regard to plant populations it is also clear that ecotypic differentiation is the rule rather than the exception. It is really difficult in a search of the literature to find examples of phenotypically or ecologically distinct populations that do *not* show genetic differentiation. Such cases would be well worth documenting, even though workers in the past may have been reluctant to do so.

If it is indeed insufficient to explain limits to natural selection in terms of overall genetic variation, we must look for alternative approaches. Three approaches seem particularly worthwhile at this time.

1. *Comparison of evolutionary potential.* We can look for contrasting evolutionary responses in different populations (or species) subjected to similar selective forces, and assess reasons for the differences in response. This is difficult because we know relatively few cases of evolutionary change that are sufficiently clear-cut to be amenable to such analysis. One exception is the evolution of metal tolerance in plants: already there are a sufficient number of intriguing observations and initial experiments which suggest that the comparison of evolutionary potential is a tractable approach. Screening seedlings for survival on mine soil can test if nontolerant populations contain genes for metal tolerance (Walley et al., 1974). In this way tolerant genotypes have been found not only in nontolerant populations of species that can colonize metal mines, but also in species that occur in the vicinity of mines but not on them (Gartside & McNeilly, 1974). It is relevant to ask what these genes are doing in the nontolerant populations, why they only seem to be present in some species and not others, and why some species can evolve high degrees of metal tolerance whereas others generally have a lower tolerance and are confined to less toxic regions. For example, *Plantago lanceolata* can evolve tolerance to lead and zinc (Wu & Antonovics, 1975, 1976) yet it seems unable to evolve tolerance to copper (Gartside & McNeilly, 1974); in nature it is rarely found on copper mines. There seems also to be a limit to the level of lead and zinc tolerance which it can evolve since it is only found in areas of low contamination. The grass *Agrostis tenuis*, a species renowned for its ability to evolve tolerance, is not found on certain lead mines in Scotland. Instead the mines are colonized by *Agrostis canina* (Craig, 1970). It is completely unknown why *A. tenuis* is unable to evolve tolerance on these particular mines.

2. *Comparison of highly restricted and widespread species.* It is remarkable, apart from the reference cited earlier (Babbel & Selander, 1974), that in the whole of experimental plant ecology and genetics almost nothing is known about the biology of widespread species as opposed to rare species that were formerly widespread (palaeoendemics). Various factors may contribute to this lack of information, but the primary one is probably the fact that experimental ecology and population genetics has in the past been largely the province of zoologists rather than botanists. If an animal is rare, it is almost by definition difficult to

TABLE 1. Leaf characters of *Plantago cordata*, sampled from three populations along a 3 km stretch of one stream in Davidson County, North Carolina. The means are based on twenty field collected seed families, with five plants per family, and grown in a growth chamber in a completely randomized design.

		Leaf Character		
Population	Number	Blade Length (cm)	Blade Width (cm)	Petiole Length (cm)
Upstream	6.2	19.2	7.3	8.3
Midstream	6.7	20.2	7.9	6.5
Downstream	6.5	15.6	5.9	6.5
Significance of population differences[a]	$P = 0.042$	$P = 0.14$	$P = 0.048$	$P = 0.11$

[a] Multivariate significance of population differences, $P = 0.0008$, taking into account above variables measured at two times.

locate and difficult to study without endangering the species during sampling and experimentation. Plants, however, have tremendous advantages in these respects since they can be precisely and repeatedly located (often data on herbarium sheets is adequate), they can be sampled nondestructively either from seed or from vegetative propagules, and usually they are easily grown in experimental situations. Clearly there is a tremendous potential here for future investigations.

We (Meagher & Antonovics, unpublished) have initiated a study of a rare species of *Plantago* in North Carolina, namely *P. cordata*. This species is rare but fairly widespread west of the Appalachians, but east of the Appalachians has been only recorded from three widely separated localities. One of these localities occurs in Davidson County, North Carolina, where the species is confined to a rocky shallow stream. Seeds were sampled from upstream, midstream and downstream populations, grown in the phytotron and the plants measured for a range of characters. The results (Table 1) show that, even though the species is rare, it still can undergo genetic differentiation between very local populations. This species clearly has the potential for evolutionary change, but it is clearly pertinent to ask what factor is limiting its range extension and what the genetic constraints are with regard to this factor.

3. *Comparison of marginal and central populations.* Marginal populations may be of various kinds. At a geographical level, marginal populations may be found at the periphery of a species range but more or less contiguous with it, or they may be well beyond the general species range and constitute so-called "peripheral isolates." At an ecological level there may be population boundaries at ecotones or a habitat may be marginal in the sense that the population can only maintain itself at an extremely low density. These categories are by no means completely distinct, and their identification depends largely on the level of resolution chosen by the experimenter. For example, all geographically marginal populations and many island populations (particularly where the islands are defined in an ecological rather than physical context) have boundaries that are ecotonal in nature. The nature of the evolutionary process

TABLE 2. Population dynamics of a central (field) and marginal (woodland) population of *Anthoxanthum odoratum* in Durham, North Carolina (after Grant, 1974).

		Central	Marginal
Population density (plants/sq m)		15.8	1.6
Population size (mature individuals)	1972	161	24
	1973	128	29
	1974	99	20
Mortality rate (%)	1972–3	32	77
	1973–4	52	76
Recruitment rate (%)	1972–3	15	76
	1973–4	38	65

going on in these various circumstances are undoubtedly different, and a study of all of them can contribute to our understanding of limits to natural selection.

I want in this paper to concentrate especially on the problem of limits to natural selection in ecologically marginal populations and to consider in some detail the processes that may be acting to limit a species range extension in ecotonal situations. My reason for concentrating on this aspect of the subject is largely the fortuitous result of a long-standing involvement with processes that occur at ecological boundaries. But I hope to demonstrate that some of the processes are much more generally applicable to other evolutionary situations. Intuitively it is easy to understand the problem at ecotones: given that environmental parameters (climatic, edaphic, or biotic) change gradually at a boundary, why are some species unsuccessful in entering into another habitat when there is seemingly no barrier to such invasion? Two hypotheses have usually been put forward to explain such limits. The first we have already considered, namely, lack of genetic variation. The second is that gene flow from the parent population acts to prevent genetic differentiation and hence range extension across the ecological boundary. This hypothesis has been strongly counterargued by myself (Antonovics, 1968; Dickinson & Antonovics, 1973) as well as other workers (e.g., Jain & Bradshaw, 1966; Ehrlich & Raven, 1969; Endler, 1973). In brief we are left without a satisfactory view on limits to natural selection.

THE NATURE OF ECOLOGICALLY MARGINAL POPULATIONS

Before itemizing and examining in detail each of the constraints that may limit range extension, it is necessary to define the nature of a marginal ecotonal population more explicitly. It is easiest to define a marginal population, as will be done here, in terms of actual density. Any population can be considered marginal if its density falls consistently along an ecological gradient till it becomes effectively zero and the species disappears. However, it would be extremely desirable to consider a marginal population in more explicit demographic terms. It is possible to visualize several regions in an ecotonal situation:

1. A region of density dependent control, where the population is essentially at carrying capacity,

2. A region where mortality is so great that the death rate exceeds the birth rate, but equilibrium is maintained by immigration from adjacent areas of greater density,

3. A region where there is survival but no reproduction, i.e., the population is maintained solely by a balance between immigration and mortality. In this region, by definition, genetic variance in fitness is zero, since fitness is zero.

Perhaps more important than recognizing degrees of mortality may be understanding the nature of the factors which change the population density. What form these factors take depends in part on our view of population regulation. For example, the change may be an increase in the severity of density-independent effects, a change in the number of "safe-sites," or a change in the severity of density dependent effects. The latter may be particularly important in limiting a population since the central population may be already "maximally adapted" (we will return to this concept later) in terms of the density it can sustain and therefore an adjustment to a more severe action of those same factors may be particularly difficult.

This problem is illustrated by the work of Grant (1974), in a study of the grass *Anthoxanthum odoratum*, across a field-woodland ecotone. *Anthoxanthum odoratum* was abundant in the field, but its density declined into an adjacent pine woodland, till beyond about 30 m into the woodland no more plants of *A. odoratum* could be found. There were clear differences in both density and rates of population turnover between central and marginal populations (Table 2); as expected, the turnover in the marginal populations was greater. Nevertheless, population size in this marginal site remained remarkably constant over three years, suggesting some form of density dependent regulation. This regulation must have been acting at a safe site or predator dependent level since individuals were widely spaced ($1.6/m^2$) with plant-plant interactions very unlikely. However, in the central region it seemed clear from the density of the population that plant-plant interactions were important. In other words, the marginal population did not simply have to adjust to more severe density independent factors, nor to an accentuation of existing density dependent factors, but seemed to be regulated in a completely different way from the central population.

Constraints on Range Extension

selection on several characters simultaneously

Fitness is a complex trait made up of many components: when a population migrates to a new habitat, there is frequently simultaneous selection for many traits. For example, mine and pasture populations of *Anthoxanthum odoratum* differ in many characters (see Antonovics & Bradshaw, 1970). Knowing the mean of the traits in the mine populations, and the mean and variance of traits in the pasture population from which the mine population was derived, it is possible to calculate (Van Valen, 1965) the selection pressure on each character that would be needed to effect a shift from pasture to mine traits in one genera-

TABLE 3. Potential intensity of selection on individual characters during colonization on mine soil by a pasture population of *Anthoxanthum odoratum*. Overall selection pressure on morphological traits is very high. (See text for explanation of assumptions on which these calculations are based.)

Character	Pasture $\bar{x}$	Pasture s.d.	Mine $\bar{x}$	Mine s.d.	Standard Deviations of Change From Pasture to Mine	Selection Pressure
Index of tolerance (%)	8.8	10.56	75.4	23.81	6.31	ca. 0.9999
Self-fertility (log # seeds)	0.051	0.12	0.156	0.19	0.88	0.55
Flowering time (days after 9/5/1966)	21.3	5.22	17.3	4.39	0.77	0.48
Height (cm)	53.4	10.35	39.6	5.41	1.33	0.70
Flag leaf length (mm)	32.8	8.06	25.4	5.04	0.92	0.57
Number of inflorescences	79.2	36.3	52.6	32.83	0.73	0.46
Overall selection pressure on traits other than tolerance (assuming traits act independently and effect on fitness is multiplicative) =						0.9837

tion (see Table 3). This calculation is grossly over-simplified since it assumes, among other things, that we are measuring additive genetic variance, and I therefore use it only for the sake of illustration. If we assume that each character contributes multiplicatively to fitness, and that the characters are independent, then we can calculate the selection pressure which would be needed to effect a simultaneous shift in all characters, from the product of the individual fitness (Table 3). We can see that although the selection pressure on each morphological trait individually is moderate, a very large selection pressure would be needed to change all the traits simultaneously. The inverse of this value is equivalent to the probability of finding a typical mine genotype in the pasture population. If we include metal tolerance in the calculations, the probability that the pasture population will produce a perfectly adapted mine genotype becomes extremely low. From these considerations we are left with an intriguing dilemma: the lower the probability that an appropriate variant ("mine genotype") can be produced, the greater will be the selection pressure tending to preserve it.

The studies of Grant (1974) mentioned previously provide us with a more realistic view. He sampled *Anthoxanthum* adults as single tillers from three sites across a field-woodland ecotone; he termed the populations at these sites the central population (in the field), the ecotonal population (at the woodland margin itself), and the marginal population (in the woodland). These single tillers were multiplied up in the greenhouse and reciprocal transplants carried out between the field, ecotonal and woodland sites. The transplants were placed into

TABLE 4. Survivorship, seed output per survivor, and relative fitnesses of central (field) and marginal (woodland) populations of *Anthoxanthum odoratum* transplanted reciprocally as adult tillers into the central and marginal habitats.

Habitat		Population	
		Central	Marginal
Central (Field)	Survivorship =	79%	53%
	Seed number =	197	74
	Relative fitness =	1	0.25
Marginal (Woodland)	Survivorship =	36%	86%
	Seed number =	59	62
	Relative fitness =	0.14	0.34

pots sunk in the ground, and the pots contained soil of the site into which the transplants were made so as to simulate field conditions closely, yet insure a reasonable survivorship. The results showed that there were genetic differences between the marginal population and the central population for many traits, and each population did best in its own habitat in terms of the fitness components, seed set and survivorship (Table 4). The ecotonal population was generally intermediate in character to the central and marginal and is not included in Table 4 nor in most of the subsequent discussion.

This kind of experiment permits an interesting sequence of comparisons which serve to illustrate the complexity of changes that occur when a population moves into a new habitat (Fig. 1). A comparison of the central population in the central habitat with the central population in the marginal habitat represents the phenotypic response of the central population to the new habitat immediately after migration. (Clearly adult tillers cannot migrate, but this experiment could be readily carried out with seed progeny.) If we now compare the central population in the marginal habitat with marginal population grown in the marginal habitat, then this represents the genotypic or evolutionary response of the central population following migration into the new habitat. Finally, it is possible to compare the marginal population in the marginal habitat with the marginal population in the central habitat. This tells us if there are characters which appear to be the same in the marginal and central populations (when both are grown in the marginal habitat) yet which have undergone genetic change in the marginal habitat: these characters would probably not remain the same when returned to the central habitat. Figure 1 includes all the characters that showed significant differences in at least one of the above comparisons. Firstly, there is a change in many characters. Secondly, the central population can seemingly adapt phenotypically as far as several traits are concerned, but this phenotypic change becomes genetically fixed, presumably because the phenotypic plasticity involves some cost (either energetic or as a result of phenotypic correlations reducing fitness). Thirdly, phenotypic response is usually in the same direction as genetic response. A system of reciprocal transplants done under field conditions, and

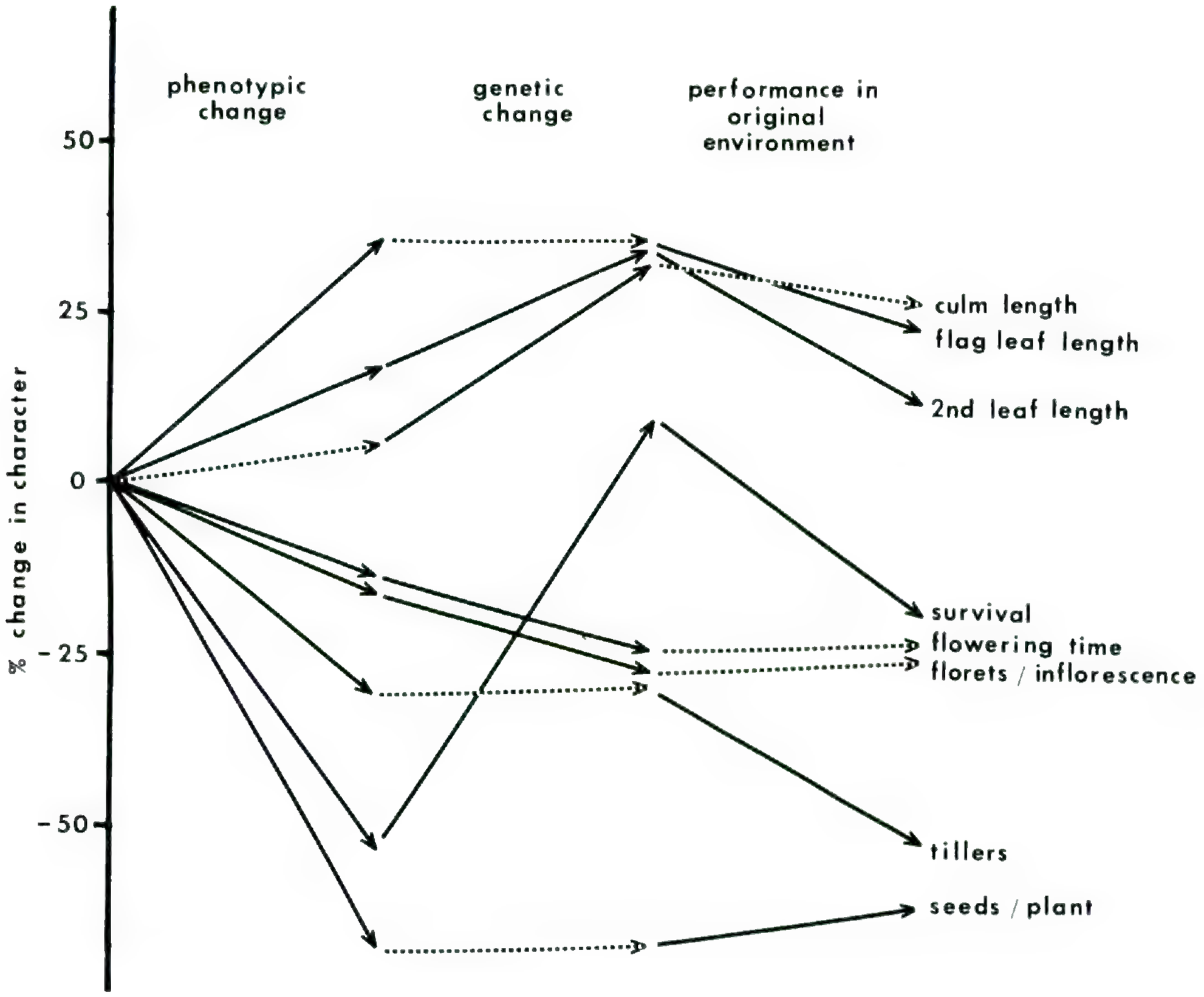


FIGURE 1. Diagram showing the phenotypic and genetic changes in a range of characters when a central (field) population of *Anthoxanthum* migrates into a marginal (woodland) habitat. The changes are expressed as percentages of the measure of the character in the central population in the field habitat; solid lines represent statistically significant ($P < 0.05$) changes. The data is calculated from the transplant experiments of Grant (1974). Phenotypic change is represented by a comparison of the central population in the field with the same population in the woodland; genotypic change is calculated by a comparison of the central population in the woodland with the marginal population in the woodland; and performance in the original environment represents the comparison of the marginal population in the woodland with the same population in the field.

using rigorous experimental design, can therefore provide us with a large amount of information about selection processes, how they interact with phenotypic responses, and how different characters interact in selection responses. When combined with realistic fitness estimates based on survivorship and fecundity, and extended to seedling-adult comparisons to estimate on-going selection pressures, this simple and in fact rather old-fashioned genecological approach can become very powerful.

The effect of simultaneous selection on several characters will depend on how these characters are correlated with each other genetically, and how they are correlated with regard to their effects on overall fitness. There are two fundamental, but often poorly appreciated, tenets of quantitative population genetics which arise from considering the effects of directional selection on a quantitative

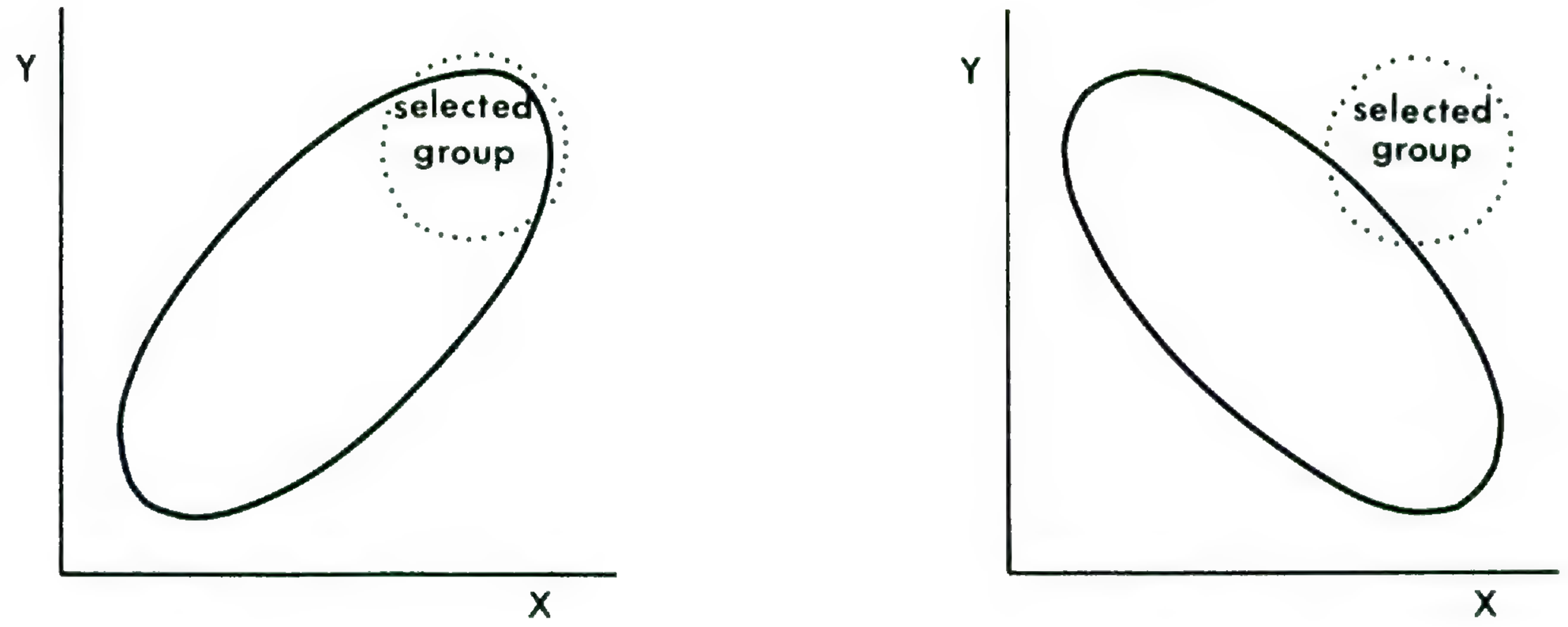
trait. The first is that there will be a rapid reduction in the additive genetic variance of the character undergoing selection. This is sometimes translated into the "law" that the greater the contribution of a character to fitness, the less will be the genetic variance in that character. This generalization requires the assumption that there is only directional selection operating: under various forms of balancing selection there can be considerable genetic variation in an adaptive trait. The second tenet is that there will be rapid selection for (and hence rapid fixation of) genes that contribute to characters having a strong positive genetic correlation with regard to their effect on fitness. Genetic correlation results either from pleiotropic gene action or from linkage disequilibrium. The relationship between selection for two traits simultaneously and their response to selection can be stated (after Falconer, 1960) as follows:

$$R_x = S_x h_x (h_x + r_{xy} h_y)$$
$$R_x = S_y h_y (h_y + r_{xy} h_x)$$

where x,y = two traits under selection (expressed as standardized scores, i.e., with mean = 0, standard deviation = 1); R = response to selection (change in mean of selected group); S = selection differential (mean of group selected); h^2 = heritability (additive genetic variance/phenotypic variance); r_{xy} = genetic correlation of x and y. In other words, even though each trait individually may show genetic variance, if they are negatively correlated ($r_{xy} < 0$), they will show a reduced selection response. If the negative correlation is –1, then clearly there will be no response to selection by either character. This is illustrated diagrammatically in Fig. 2.

As a result of these two tenets, we would expect a natural (as well as an experimental) population undergoing selection to show a reduced genetic variance for fitness traits, and a negative correlation among components contributing to fitness since genes or gene combinations contributing positively to several fitness components will be rapidly fixed in all members of the population (see Falconer, 1960: 328 for discussion). A negative correlation among fitness traits is often evidenced in plant populations. Intuitively we might think that larger plants live longer and have more fruits per inflorescence, and more or bigger seeds. However, if we look at field-collected plants, negative correlations between the fitness components are often evident (Table 5). Such negative correlations are well known to plant and animal breeders (Adams, 1967; Grafius, 1961; Grafius & Thomas, 1971) but have been infrequently studied in natural populations.

When a population enters a new habitat, the nature of the character correlations may change in very crucial ways. If the character that is advantageous in the new habitat is not negatively correlated with any of the other characters influencing fitness (i.e., there is a new correlation among the fitness components), then evolutionary response may be rapid and relatively easy. For example, in those plants that are successful in colonizing mine soils we might predict that the property of tolerance is relatively independent of other characters. Indeed, Antonovics & Bradshaw (1970) found that tolerance in *Anthoxanthum odoratum* was not correlated with any of the traits they measured when considered on a within-population basis. On the other hand, evolutionary re-



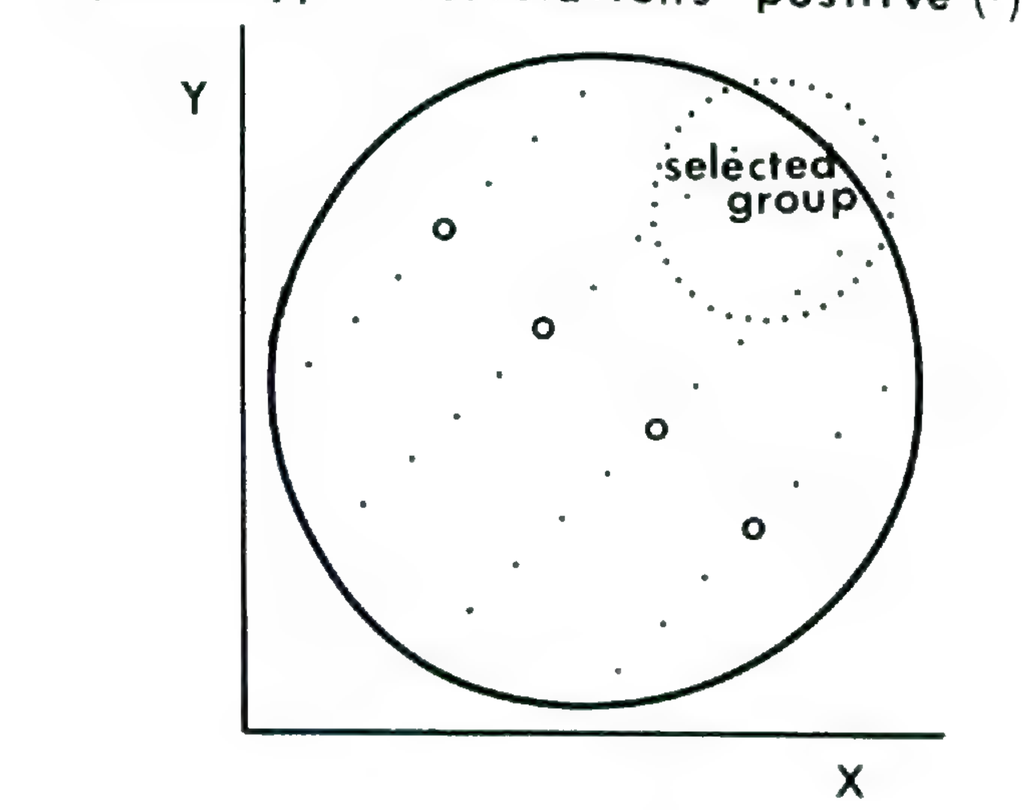


FIGURE 2. Schematic diagrams showing the effect of genetic and phenotypic correlations between two characters x and y on the response to selection. The solid ellipse or circle represents a frequency isocline of a bivariate normal distribution.—a. There is a positive genetic correlation between the characters with regard to their effects on fitness. Selection for one character reinforces selection for the other; the selected group is large and response to selection rapid.—b. There is a negative genetic correlation between the characters with regard to their effects on fitness. Selection for increased fitness in one character is counteracted by correspondingly lowered fitness in the other character. The probability of obtaining individuals which have a high expression for both characters is low; the selected group is small, and response to the same criteria of selection as in diagram a is slow.—c. Phenotypic correlations may mask the effects of genetic correlations, giving apparently a larger selected group but still a slow selection response. (For further discussion, see text.)

sponse to the new habitat may be difficult if in that habitat characters are favored which have a strongly negative effect on other fitness components, i.e., if the existing "correlation structure" of fitness components is maintained. For example, *A. odoratum* may successfully colonize a woodland by increasing its photosynthetic efficiency, by increasing its energy contribution to reproduction (and not competition as in the field), or by changing leaf area. There is evi-

TABLE 5. Phenotypic correlations among fitness components of individuals of a central (field) and marginal (woodland) population of *Anthoxanthum odoratum*. Correlations are based on twenty individuals from each population measured in the field under natural conditions. Flowering time refers to date of flowering, i.e., a positive correlation with the numerical traits indicates that later flowering individuals had more of that trait. (Correlations expressed as %, where values greater than 44 or less than –44 are significant, P = 0.05.)

CENTRAL POPULATION	SEED #	TILLER #	INFLORESCENCE #	SPIKELETS / INFLO	SEEDS / INFLO	FLOWERING TIME
SEED #		89	53	32	-61	51
TILLER #	63		93	35	40	-76
INFLORESCENCE #	32	77		71	46	-94
SPIKELETS / INFLO	35	-43	23		29	-27
SEEDS / INFLO	29	-40	-27	-2		-40
FLOWERING TIME	52	-83	-91	-23	55	

MARGINAL POPULATION

dence (Grant, 1974) that marginal woodland populations indeed have a higher chlorophyll *b*/chlorophyll *a* ratio and are therefore more shade tolerant, devote more energy to reproduction, and have larger flag leaves. Yet these characters are clearly in conflict with other attributes since survivorship of woodland plants is low, and their reproductive output is only somewhat greater than that of field plants transplanted into the woodland (Fig. 1).

Numerous aspects of selection in natural populations still need to be studied:

1. How does selection on several individual traits contribute to overall fitness? Does it contribute additively, multiplicatively, or in some more complex fashion to overall fitness? How does it depend on the correlation among the characters?

2. How can we define fitness in demographic terms? Concepts of reproductive value, quality of seed (inbred/outbred), and degree of relatedness of competitors are all important and deserving of study in plant populations.

TABLE 6. Number of correlations that are significant at $P < 0.001$ or in parentheses, $P < 0.01$, among nine characters measured on the 10th leaf of four different varieties of climbing beans, *Phaseolus vulgaris*, grown under three temperatures. Characters are petiole length, length of petiole of terminal leaflet, length and width of two lateral leaflets, and length and width of left and right halves of the terminal leaflet. Each correlation is based on twelve plants; a total of thirty-six correlations are possible for each variety at each temperature. Mexican A and B are two wild varieties from Mexico.

	Temperature (Day/Night)		
Variety	26°/23°C	23°/20°C	20°/17°C
Kentucky Wonder	34 (2)	33 (3)	4 (3)
Half Runner	1 (3)	9 (8)	8 (9)
Mexican A	15 (6)	1 (1)	1 (13)
Mexican B	1 (4)	2 (2)	7 (5)

3. How do widespread versus restricted species differ with regard to the degree of correlation among fitness components? It is well known (see also Adams, 1967) that levels of correlation between characters differ between strains, and are also influenced by the environment (Table 6). Do more restricted species show a greater interdependence of their characters? If so, how has this come about? Does specialization (strong directional selection towards a particular optimum) lead to stronger character interdependence?

4. What is the relationship between directional selection for fitness traits and stabilizing selection (or some other forms of balancing selection) on component traits?

5. How does the relationship between genetic and phenotypic correlation between characters influence selection on these characters? It is often clear that an individual may show positively correlated phenotypic responses (e.g., get larger in many traits as a result of being grown in a favorable environment), yet show negatively correlated genetic responses (e.g., selection for larger leaves generally results in a slower rate of leaf production; Edwards & Cooper, 1963; Edwards, 1967).

6. What are the consequences of gene flow between populations differing in direction and magnitude of character correlations?

7. What is the relationship between within-species correlations and between-species correlations? Does taxonomic diversification occur more frequently along within-species correlation axes, and is it rarer to have taxonomic diversification in an opposite direction? There is evidence in many plant and animal groups that between-species correlations may be either in the same or opposite direction as within-species correlations (Fig. 3).

The problems inherent in assessing the relative fitness of different genotypes and in measuring heritability and genetic correlations are formidable. But it seems that understanding the variance-covariance structure of fitness traits is essential if we are to get away from a simplified view of genetic variation in natural populations. *Anthoxanthum odoratum* in pastures, woodlands, and on mines is genetically variable for numerous quantitative traits: the im-

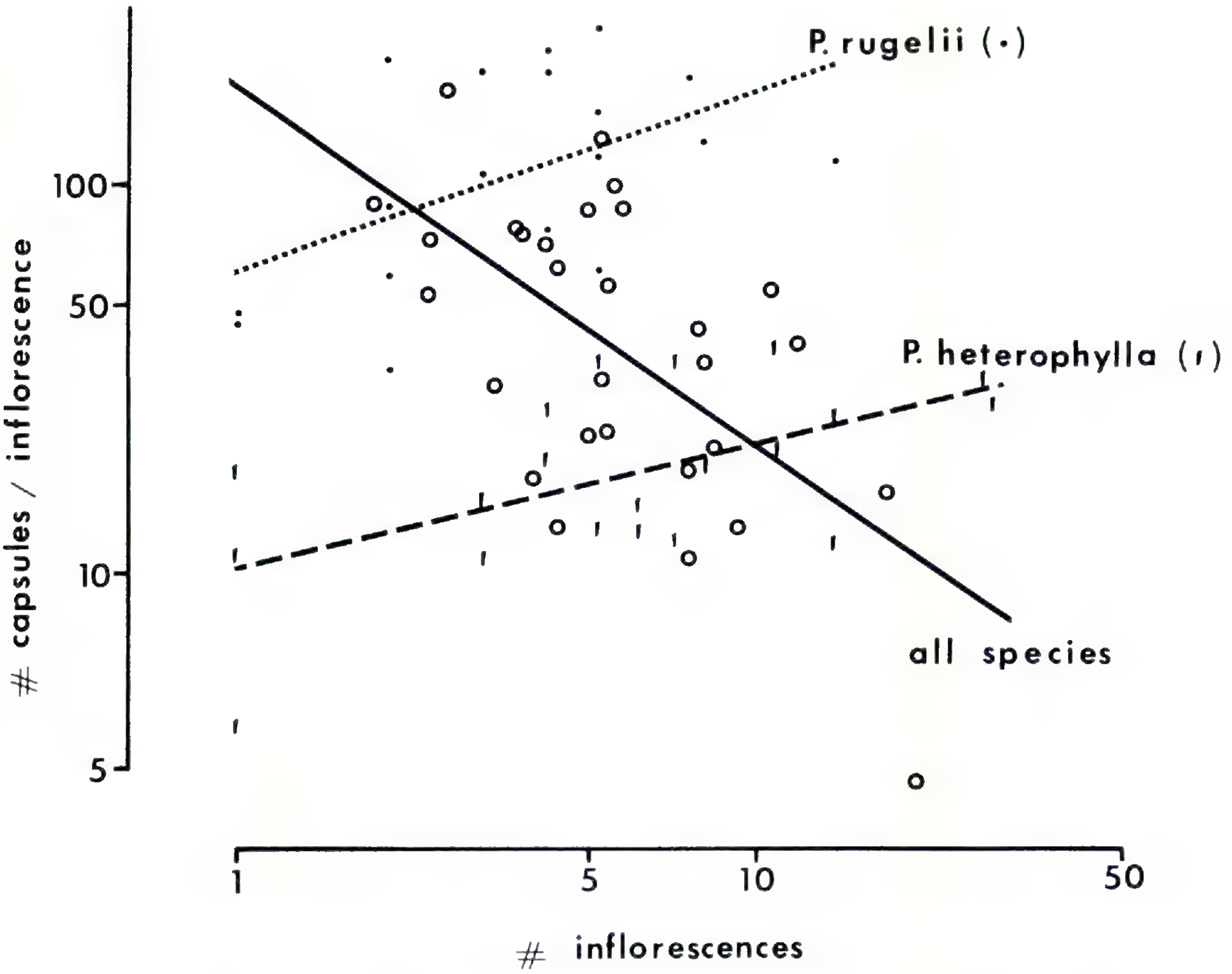


FIGURE 3. Graph showing the between-species correlation for a pair of characters (number of inflorescences and number of capsules per inflorescence) in the genus *Plantago*, and the within-species correlations for two particular species. The between-species correlation was highly significant ($P < .01$). Of the within-species correlations, 27 were positive (11 significantly so, $P < 0.05$) and only 6 were negative (none significantly so). Each within-species correlation and each value for a species mean (circles) is based on approximately twenty well-preserved herbarium specimens from a wide range of localities (data from R. Primack, unpublished).

portant question is not how much variation there is, but how that variation is constrained. The fact that variation is in some sense constrained has been long appreciated in the notion of coadapted gene complexes (Dobzhansky, 1951). The concept has been in large measure philosophical if not simply "felicitous" (Mayr, 1963: 272), being based on observations that crosses between similar phenotypes from different populations may result in hybrid breakdown, that the expression of a gene is dependent on its genetic background, and that different inversion karyotypes become adjusted to each other in experimental populations. It has had little operationality in that it has been impossible to measure or quantify "degree of coadaptation." Recently there has been an increasing interest in quantifying "coadaptation" at the gene level and a search for nonrandom gene association along chromosomes. Taxonomists (Sokal & Sneath, 1963) and palaeontologists (Olson & Miller, 1958) have approached their subjects from a multivariate context, and it seems that defining "coadaptation" at the phenotypic and genotypic level will require that natural selection be looked at from a similar standpoint.

TABLE 7. Effect of different character correlations among fitness components on selection in a finite population. For explanation, see text and Grant (1974).

Correlation Matrix	Generations to Max. Fitness	Number of Extinctions
1 +0.6 0 1 0 1	4.6	1
1 –0.6 0 1 0 1	15.3	17
1 –0.2 –0.2 1 –0.2 1	28.1	7
1 –0.2 –0.2 –0.2 –0.2 1 0 0 0 1 0 0 1 0 1	16.1	5

SMALL POPULATION SIZE

Frequently marginal populations are either physically small (peripheral isolates) or show a reduction in density (ecotonal populations). This can have several consequences:

1. Given that selection acts on many characters and that adaptation may be required in many characters simultaneously, there may be a real problem, if the population is small, of obtaining genotypes with the appropriate combination of characters. Grant (1974) developed a stochastic model of selection on a multivariate character. The results showed that in a population of 50 individuals extinctions could readily result if selection demanded new combinations of characters that were themselves negatively correlated (Table 7). Several small negative correlations could have as serious an effect as a few large negative correlations, a rather disheartening conclusion in view of the sample sizes needed to detect small correlations as being statistically significant. (For example a correlation between two traits of 0.2 would require a sample size of the order of 100 to be deemed significant: for the estimation of genetic correlations far larger sizes would be needed.)

2. Gene flow into a peripheral isolate would be largely dependent on its degree of isolation. In an ecotonal population, however, a lower density of marginal individuals would increase the swamping effect of gene flow (this is discussed later).

3. In a population that is small there will be a high probability of mating between relatives and a possibility of severe inbreeding depression effects. In a population subject to strong selection these inbreeding depression effects may be more severe (Latter & Robertson, 1972). This is well illustrated in the work of Ford (1973). In competition experiments between wild type and Bar eye mutant *Drosophila*, he maintained lines where Bar was permitted to interbreed

with wild type, and lines where interbreeding was not permitted. In the interbreeding lines the competitive ability of Bar increased over controls. In the non-interbreeding lines, where the improvement of competitive ability of Bar might have been expected, there was actually a decline. This was interpreted as being due to inbreeding plus strong selection due to competition with the wild type: when the separated wild type and Bar lines were crossed there was an immediate increase in the competitive ability of Bar (see Fig. 4). Precisely why populations should show inbreeding depression for fitness traits is not clear to me and, even given the extended arguments of the 1950's, I feel it has never been satisfactorily explained. Perhaps consideration of genetic variation in natural populations may throw light on this dilemma, since much of the earlier experimental work was agronomically oriented. Above all, inbreeding depression, whatever its precise mechanism (dominance of favored genes, overdominance, "relational balance," or variance in regulatory genes) must have an evolutionary explanation, and it must in some way be related to the forces that mold fitness components.

GENE FLOW

The role of gene flow in natural populations remains an enigma. Several years ago it was considered to be a cohesive force in evolution, and was central to the concept of a species and how speciation occurs. Demonstration that selection could overcome the swamping effect of gene flow opened up the controversy of whether sympatric divergence and sympatric speciation was possible, and, as a corollary, whether it was common. Subsequent emphasis on the limited extent (Ehrlich & Raven, 1969; Levin & Kerster, 1974) and limited effectiveness (Endler, 1973) of gene flow raised an issue very disturbing to taxonomists: why, given the limited extent of gene flow, were species still relatively uniform? It is pertinent therefore to ask what role gene flow plays in limiting natural selection.

It seems to have been underemphasized that gene flow will have drastically different effects depending on whether the genes concerned are effectively neutral, advantageous, or mildly deleterious in the population into which they migrate. If the genes are neutral, their spread, particularly if the population structure is viscous (as in many plants, see Levin & Kerster, 1974), will be very slow. If the genes are advantageous, they will not only spread in the local population but will migrate and spread into other populations. This process can be very effective and very rapid. For example, if we assume that dispersal follows a leptokurtic distribution of the form, $y = x^{-k}$, where x is the distance and k is some constant, it is possible to estimate at what distance from the source the migration rate will be equivalent to the mutation rate. Taking the function $y = x^{-1.5}$, where x is in meters, and a migration rate of 10^{-5} as equivalent to a mutation rate, then we find that even if the population into which the new allele is migrating is over 2 km (2,154.4 m) away, the migration rate will still be greater than the mutation rate. The dispersal function chosen is rather conservative, giving a dispersal of 3% of the source at about 10 m—a figure typical of many grasses. The process of spread of favorable genes across the geographical range of a species

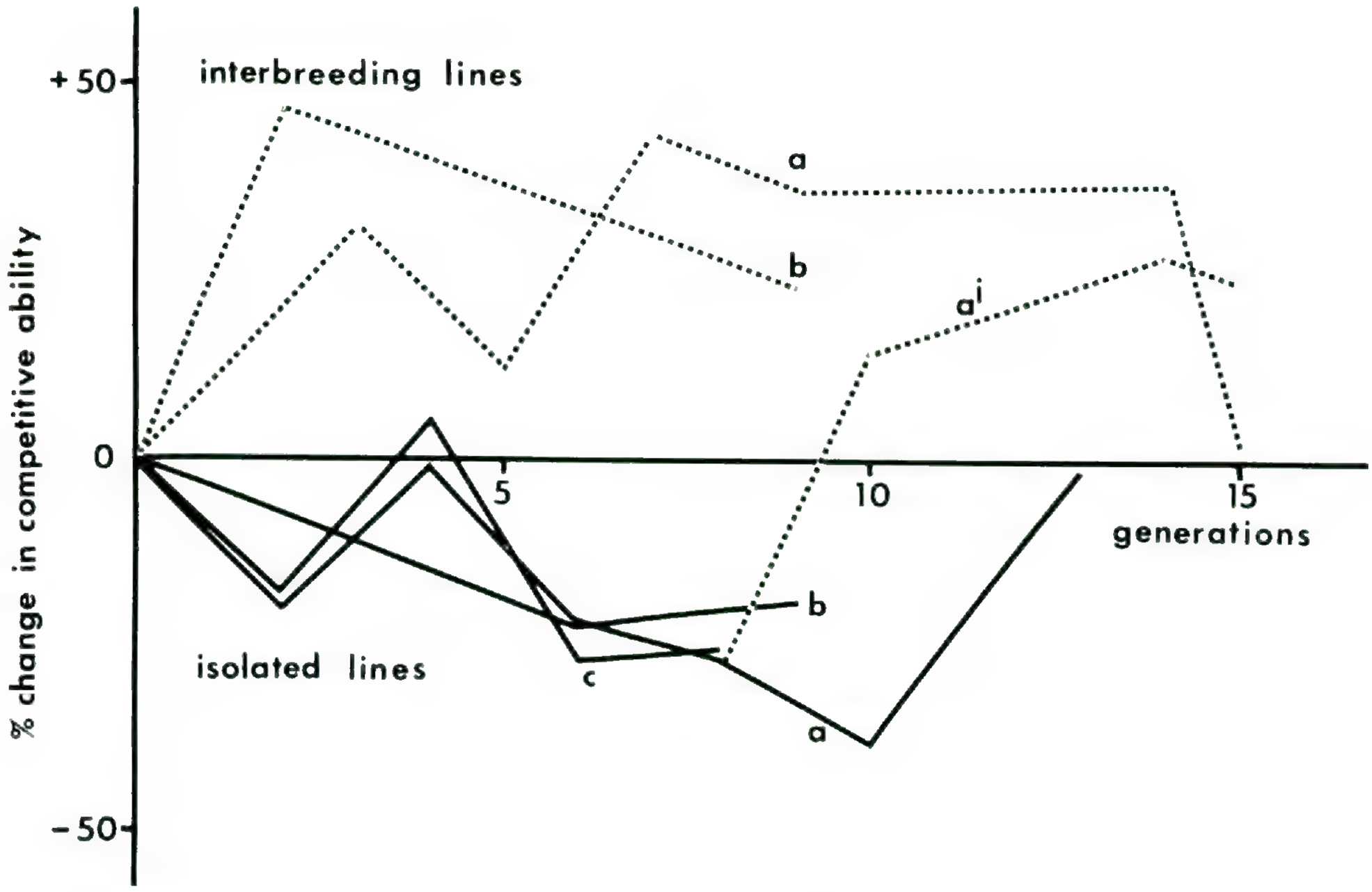


FIGURE 4. Change in competitive ability of Bar strains of *Drosophila melanogaster* tested in competition against control wild type *D. melanogaster*, following experience for a certain number of generations in isolated and interbreeding mixtures with wild type strains. The different lines refer to different experiments. Lines *a* and *c* were started from general laboratory stocks of Bar and wild type. Line *b* was started from a Kaduna strain into which Bar gene had been introduced and maintained polymorphic for 30 generations by J. Endler. In the isolated lines only within-type matings were allowed. In the interbreeding lines random mating was allowed and an equal number of wild type or Bar homozygous female parents was used to continue the next generation: heterozygous Bar parents were discarded. In each generation of both, the isolated lines and interbreeding lines were started using 10 females of each type. In *a*, a rotating mating scheme was used where half the flies from a given replicate were included with another replicate and so on. In *b*, there were four independent replicates. In *c*, there were ten independent replicates. (Data from Ford, 1972.)

has been considered more rigorously by Fisher (1937), Moran (1962) and Cavalli-Sforza et al. (1971: 485). They show that the rate of spread of a favorable gene will be approximated by the equation

$$v = \sigma\sqrt{2s}$$

where v = velocity of a point at which gene frequency has a prescribed value; σ = standard deviation of the dispersal distribution assuming the latter is normal; s = selective advantage of the favored allele. Given a mean dispersal distance of 10 m, a selective advantage of 0.1, we get a velocity of spread equivalent to 4.47 m per generation. It can be seen from the equation that the rate of spread is directly proportional to the dispersal distance. In a population that disperses 50 m on average, the rate of spread will be 20.1 m per generation. These rates of spread are calculated on the basis of a normal dispersal function; with a leptokurtic pattern, they would undoubtedly be greater. Gene flow of favorable genes can therefore occur relatively rapidly, and genes that are beneficial to many

populations of a species will be readily disseminated throughout that species range.

In an ecotonal situation, where population density declines, the levels of gene flow may be very different from that expected from a study of dispersal patterns. One can readily simulate the effects of density on gene flow using a highly iterative computer model. The model assumes the individuals are in a rectangular grid and that the central population has a high density of individuals, whereas the density in the marginal population declines as some function of distance away from the central population. At any point in this grid, one can estimate the amount of pollen received from the central population and the amount from the marginal population, assuming dispersal from each individual follows a particular function describing dispersal from a point source. In the results described here, this function is assumed to be $y = x^{-1.5}$, where y is amount of dispersal and x is distance in meters. This function closely approximates dispersal distances for many wind-dispersed herbaceous plants (for review see Raynor & Ogden, 1965). The ratio of central/total pollen received is a measure of gene flow from the central population into itself or into the marginal population. The results show that gene flow into the marginal population will be very high if the density of the individuals in the marginal population declines rapidly. Given a very rapid decline in density, we can get situations where gene flow actually increases with distance and is greater at the periphery than near the boundary of the central and marginal population (Fig. 5). Applying this model to the populations studied by Grant (1974) we find that, whereas dispersal from the central habitat falls off rapidly into the ecotonal and marginal areas, gene flow is actually greater in the marginal population than in the ecotonal. The swamping effects of gene flow can therefore be very real and substantial (e.g., Antonovics, 1968).

Gene flow might be expected to have interesting interactions with selection for character complexes. If there is selection for multiple traits, then the selection pressures in the marginal habitat are likely to be severe. Given that a substantial fraction of the variants in the marginal population is adapted to the new habitat with regard to many of their traits, this selection is likely to overcome the effects of gene flow. However, it may be that the gene flow prevents adaptation with regard to many traits simultaneously: this idea has frequently been expressed in the idea that gene flow results in "a relentless destruction of suitable new gene complexes" (Mayr, 1963: 524). The result will depend not simply on the intensity of gene flow or on the intensity of selection; it will also depend on the variance-covariance structure of the component characters in the two populations. The impact of gene flow on such complexes is in need of study and documentation in model systems as well as in natural populations.

COEVOLUTIONARY RESISTANCE

A population entering a new habitat will meet new competitors and new predators: adaptation to these will be different from adaptation to abiotic conditions since coevolutionary responses of competitors, predators, and parasites may counteract adaptive responses on the part of the species undergoing range extension. Character displacement has been well known (Brown & Wilson, 1956)

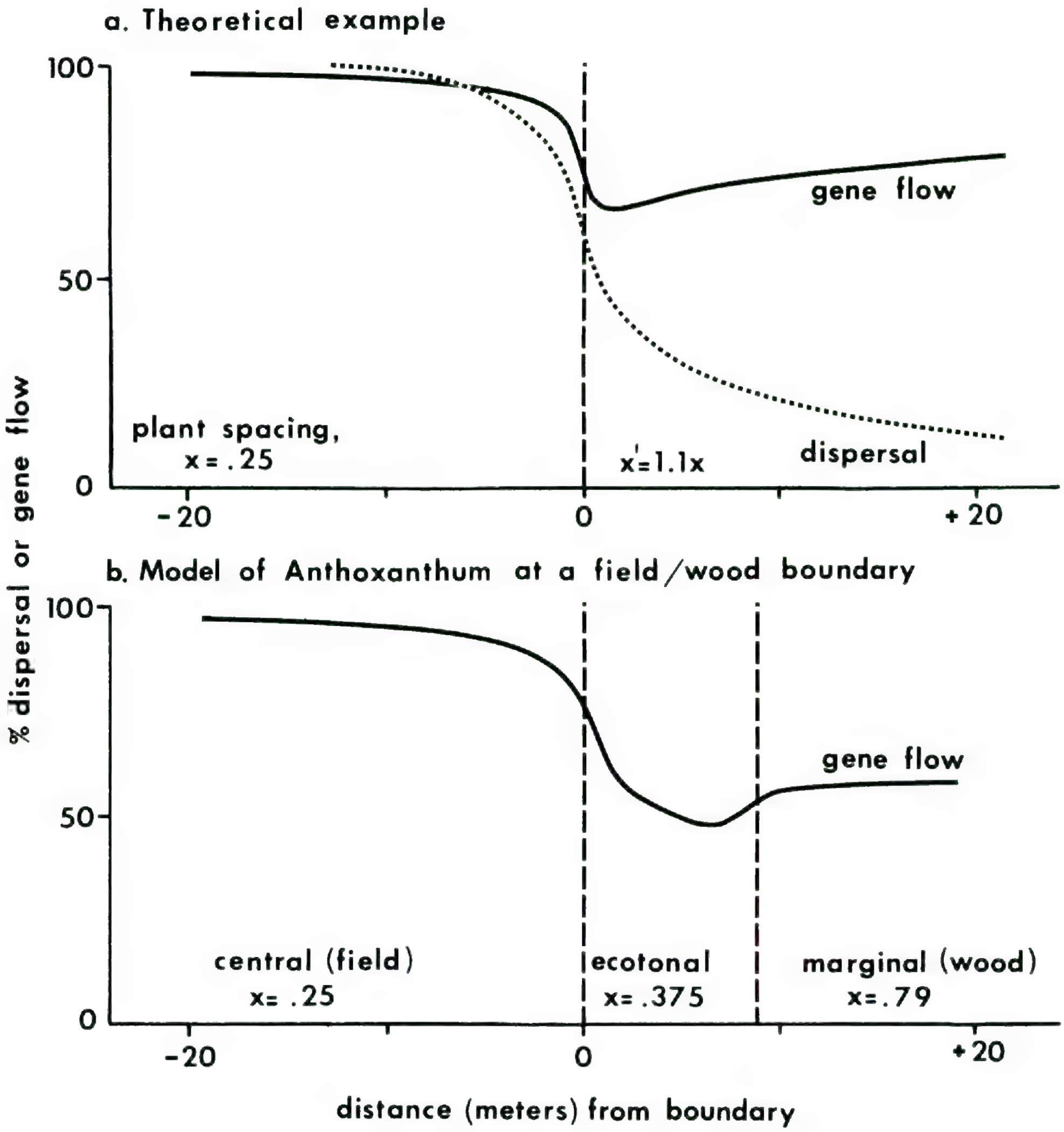


FIGURE 5. Graphs showing the effect of density on gene flow, when population density decreases at increasing distances from a habitat boundary. Data is based on a computer simulation explained in the text. It assumes a point-source dispersal function of $y = x^{-1.5}$ where x is in meters. Plants are assumed to be spaced in a rectangular grid, separated by different distances, x.—a. Theoretical model assuming that on the left-hand side of the boundary, the plants are at a density of $16/m^2$, and that to the right-hand side their spacing increases (density decreases) by the iterative relation $x' = 1.1\ x$, i.e., the plant-plant spacing between any two rows or columns is 1.1 times that of the spacing between the previous rows or columns. Dispersal from the central (left-hand) population is measured as the number of propagules, say, pollen arriving at any one point expressed as a percentage of the maximum amount of pollen produced. Gene flow is measured as the amount of pollen from the central population expressed as a percentage of the amount of pollen from the central plus that from the marginal population.—b. Model based on actual data obtained from *Anthoxanthum odoratum* at a field/wood boundary (see Grant, 1974, and text for discussion). The plant-plant spacings (x) closely approximate field observed densities of 15.8, 7.1, and 1.6 plants/m^2 for the central, ecotonal, and marginal populations. Otherwise the assumptions of the model are as above.

and the subject of much discussion among zoologists: as pointed out by Grant (1972), character displacement may take many forms and is essentially any evolutionary change that results from competitive interactions among species. Nevertheless, it is remarkable that apart from the evolution of *Camelina* in flax fields (quoted in Stebbins, 1950: 123) and instances of reproductive character displacement (Grant, 1966; Levin & Kerster, 1967; McNeilly & Antonovics, 1968) there have been virtually no studies of evolutionary changes in plant-plant competitive relationships. There are probably several reasons for this. Systematists tend to study characters that are relatively invariant with regard to ecology. Adaptive characters in plants are frequently physiological and difficult to study without special techniques. There is also often no way of telling whether minor changes in a character are due to phenotypic or genetic effects: in animals it can often be assumed with a fair degree of confidence that morphometric changes have a genetic basis. And it is not till recently that competition experiments have been refined to the point where they can be used to define population interrelationships in general ways (De Wit, 1960; Khan et al., 1975; Hall, 1974) without recourse to detailed analysis of the mechanistic aspects of competition.

We therefore must turn to experimental evidence with regard to evolutionary response to competition. The results of several recent experimental studies in this area are summarized in Table 8. They show that evolutionary responses to competitors can occur readily, but that the extent and nature of the response is very variable. By inference such changes should occur in natural populations and may be most readily detectable in ecotonal situations where community composition is changing rapidly. Their importance in limiting range extension may be considerable, particularly in view of the frequent observations that species distributions are severely limited by competition. This has long been realized with regard to water-logging (Lieth, 1960), the calciole-culcifuge problem (Rorison, 1960; Gigon, 1971), salt tolerance (Barbour, 1970) and metal tolerance (Cook et al., 1972). It is therefore all the more surprising that the evolutionary dynamics of these competitive relationships have never been studied.

Conclusion

The study of the nature of limits to natural selection has taken impetus from the realization that previous explanations were based on concepts which are erroneous (such as the unifying effect of gene flow) or essentially tautological (such as statements about genetic variance or coadaptation). The comparative ecological genetics of rare and widespread species, or of ecotonal populations, is an area that has been severely neglected creating a serious gap in our evolutionary thinking.

The present paper has indicated several factors which may all act interactively and to different degrees in limiting populations. It has been my intention not to come up with a coherent explanation of selection limits but above all to point to approaches and kinds of information that are needed to approach an understanding of this important evolutionary enigma. Many of the advances will occur

TABLE 8. Summary of a number of studies on selection for competitive ability in experimental populations (after Chen, 1973).

Author	Species	No. of Generations or Time	Evidence For: Genetic Changes in Competitive Ability	Evidence For: Increased Niche Divergence	Evidence For: Increased Yield of Mixtures	Evidence For: Changes in Associated Characters
Moore (1952)	*Drosophila simulans* & *D. melanogaster*	500 days	Good evidence	—[a]	—	—
Lewontin (1955)	*D. melanogaster*		Good evidence	—	Yes	—
Chen (1973)	*D. melanogaster*	1	Good evidence	Yes	Yes	—
Seaton & Antonovics (1967)	*D. melanogaster*	4	Good evidence	Yes	Yes	Yes
Futuyma (1970)	*D. melanogaster*	10	Some lines increased others decreased	—	—	—
Bryant & Turner (1972)	*Musca domestica*	5	Good evidence	Yes	Yes	Yes
Ayala (1969)	*D. serrata* & *D. nebulosa*	31 weeks	Good evidence	Yes	—	—
Ford (1972)	*D. melanogaster*	15	Often negative	Slight	No	Yes

[a] Means no evidence obtained.

through an increasingly demographic view of fitness and adaptation, a multivariate view of selection and adaptation, an appreciation of the nature of gene flow and inbreeding depression, and through a study of coevolutionary phenomena.

The elegance of one locus deterministic models seems to have constrained our thinking, not simply with regard to variation at the gene level, but also with regard to selection at the character level. There are, for example, no *a priori* criteria for determining how selection on different characters acts with regard to fitness, and similar problems exist in modelling multi-locus systems. It seems trite but it is unfortunately necessary to say that we need to understand selection before we can understand variation.

Since this is a symposium primarily for plant systematists, it is appropriate to end by pointing out that they have a very important role to play in backgrounding the studies outlined here. We are largely dependent on systematists for identifying rare species, identifying species ranges, and for establishing their historical status plus evolutionary affinities. We are largely dependent on systematists for accurate herbarium records and location of field sites. We are largely dependent on systematists for information on basic ecology and biology of the species concerned and their cohabitants. I hope this paper has served the dual function of perhaps interesting the systematist in that frightening, highly mathematical subject

of population genetics and the population geneticist in that highly specialized, "someone's-got-to-do-it" subject of plant systematics. Both disciplines may be less dull as a result of such interaction.

Literature Cited

Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean *Phaseolus vulgaris*. Crop Sci. 7: 505–510.

Antonovics, J. 1968. Evolution in closely adjacent plant populations VI. Manifold effects of gene flow. Heredity 23: 507–524.

———. 1975. Predicting evolutionary response of natural populations to increased UV radiation. Climatic Impact Assessment Program Monograph V. Impacts of Climatic Change on the Biosphere. Department of Transportation. Chapter 8: 3–26.

——— & A. D. Bradshaw. 1970. Evolution in closely adjacent plant populations VIII. Clinal patterns at a mine boundary. Heredity 25: 349–362.

Ayala, F. 1969. Evolution of fitness IV. Genetic evolution of interspecific competitive ability in *Drosophila*. Genetics 61: 737–747.

Babbel, G. R. & R. K. Selander. 1974. Genetic variability in edaphically restricted and widespread plant species. Evolution 28: 619–630.

Bantock, C. R. 1974. Experimental evidence for non-visual selection in *Cepaea nemoralis*. Heredity 33: 409–412.

Barbour, M. G. 1970. Is any Angiosperm an obligate halophyte? Amer. Midl. Naturalist 84: 105–120.

Brown, H. L. & E. O. Wilson. 1956. Character displacement. Syst. Zool 5: 49–64.

Bryant, E. H. & C. R. Turner. 1972. Rapid evolution of competitive ability in larval mixtures of the housefly. Evolution 26: 161–170.

Cavalli-Sforza, L. L. & W. F. Bodmer. 1971. The Genetics of Human Populations. W. H. Freeman and Co., San Francisco. 965 pp.

Chen, S. L. 1973. Selection for competition interactions between *Drosophila* strains. Master's thesis, Duke University, Durham, North Carolina.

Clarke, B. 1975. The causes of biological diversity. Sci. Amer. 233(2): 50–60.

Cook, S. C. A., C. Lefebvre & T. McNeilly. 1972. Competition between metal tolerant and normal plant populations on normal soil. Evolution 26: 366–372.

Craig, G. C. 1972. The population genetics of *Agrostis canina* with respect to lead tolerance. Master's thesis, University of Stirling, Scotland.

De Wit, C. T. 1960. On competition. Verslagen Landbouwk. Onderz. Waageningen 66: 1–82.

Dickinson, H. & J. Antonovics. 1973. Theoretical considerations of sympatric divergence. Amer. Naturalist 107: 256–274.

Dobzhansky, T. 1951. Genetics and the Origin of Species. Ed. 3. Columbia University Press, New York. 364 pp.

Edwards, K. J. R. 1967. Developmental genetics of leaf formation in *Lolium*. Genet. Res. 9: 247–257.

——— & J. P. Cooper. 1963. The genetic control of leaf development in *Lolium* II. Response to selection. Heredity 18: 307–317.

Ehrlich, P. R. & P. H. Raven. 1969. Differentiation of populations. Science 165: 1228–1232.

Endler, J. A. 1973. Gene flow and population differentiation. Science 179: 243–250.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. Oliver and Boyd, Edinburgh. 365 pp.

Fisher, R. A. 1937. The wave of advance of advantageous genes. Ann. Eugen. 7: 355–369.

Ford, H. A. 1972. Ecological partitioning by *Drosophila* populations. Ph.D. thesis, University of Sterling, Scotland.

Futuyma, D. J. 1970. Variation in genetic response to interspecific competition in laboratory populations of *Drosophila*. Amer. Naturalist 104: 239–252.

Gartside, D. W. & T. McNeilly. 1974. The potential for evolution of heavy metal tolerance in plants II. Copper tolerance in normal populations of different plant species. Heredity 32: 335–348.

Gigon, A. 1971. Vergleich alpiner Rasen auf Silikat- und auf Karbonatboden. Veröff. Geobot. Inst. Rübel Zürich 48: 1–159.

GRAFIUS, J. E. 1961. The complex trait as a geometric construct. Heredity 16: 225–228.
——— & R. L. THOMAS. 1971. The case for indirect genetic control of sequential traits and the strategy of deployment of environmental resources by the plant. Heredity 16: 433–442.
GRANT, M. C. 1974. Genetic properties of ecologically marginal populations of *Anthoxanthum odoratum*. Ph.D. thesis, Duke University, Durham, N. C.
GRANT, P. R. 1972. Convergent and divergent character displacement. Biol. J. Linnean Soc. 4: 39–68.
GRANT, V. 1966. The selective origin of incompatibility barriers in the plant genus *Gilia*. Amer. Naturalist 100: 99–118.
GREENWOOD, J. J. D. 1974. Visual and other selection in *Cepaea*: a further example. Heredity 33: 17–31.
HALL, R. L. 1974. Analysis of the nature of interference between plants of different species. I. Concepts and extension of the deWit analysis to examine effects. Austral. J. Agric. Res. 25: 739–747.
JAIN, S. K. & A. D. BRADSHAW. 1966. Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. Heredity 21: 407–441.
KAHN, M. A., P. D. PUTWAIN & A. D. BRADSHAW. 1975. Population interrelationships. 2. Frequency dependent fitness in *Linum*. Heredity 34: 145–163.
LATTER, B. D. H. & A. ROBERTSON. 1962. The effects of inbreeding and artificial selection on reproductive fitness. Genet. Res. 3: 110–138.
LEVIN, D. A. & W. L. CREPET. 1973. Genetic variation in *Lycopodium lucidulum*: a phylogenetic relict. Evolution 27: 622–632.
LEVIN, D. A. & H. W. KERSTER. 1967. Natural selection for reproductive isolation in *Phlox*. Evolution 21: 679–687.
——— & ———. 1974. Gene flow in seed plants. Evol. Biol. 7: 139–220.
LEWONTIN, R. C. 1955. The effects of population density and composition on viability in *Drosophila melanogaster*. Evolution 9: 27–41.
———. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York. 346 pp.
LIETH, H. 1960. Patterns of change within grassland communities. *In* Harper, J. L. (editor), The Biology of Weeds. British Ecological Society Symposium 1: 27–39.
MAYR, E. 1963. Animal Species and Evolution. Belknap Press, Harvard. 797 pp.
MCNEILLY, T. & J. ANTONOVICS. 1968. Evolution in closely adjacent plant populations. IV. Barriers to gene flow. Heredity 23: 205–218.
MOORE, J. A. 1952. Competition between *Drosophila melanogaster* and *Drosophila simulans* I. Population cage experiments. Evolution 6: 407–420.
MORAN, P. A. P. 1962. The Statistical Processes of Evolutionary Theory. Clarendon Press, Oxford. 200 pp.
OLSON, E. C. & R. L. MILLER. 1958. Morphological Integration. University of Chicago Press, Chicago. 317 pp.
RAYNOR, G. S. & E. C. OGDEN. 1965. Twenty-four hour dispersion of ragweed pollen from known sources. Brookhaven National Laboratory Report 957: 1–17.
RORISON, I. H. 1960. Some experimental aspects of the calcicole-calcifuge problem. I. The effect of competition and mineral nutrition upon seedling growth in the field. J. Ecol. 48: 585–599.
SEATON, A. P. C. & J. ANTONOVICS. 1967. Population interrelationships. 1. Evolution in mixtures of *Drosophila* mutants. Heredity 22: 19–34.
SELANDER, R. K., S. Y. YANG, R. C. LEWONTIN & W. E. JOHNSON. 1970. Genetic variation in the horseshoe crab (*Limulus polyphemus*), a phylogenetic "relic." Evolution 24: 402–414.
SOKAL, R. R. & P. H. A. SNEATH. 1963. Principles of Numerical Taxonomy. W. H. Freeman, San Francisco. 359 pp.
STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia University Press, New York. 643 pp.
VAN VALEN, L. 1965. Selection in natural populations III. Measurements and estimation. Evolution 19: 514–528.
WALLEY, K. A., M. S. I. KHAN & A. D. BRADSHAW. 1974. The potential for evolution of heavy metal tolerance in plants. I. Copper and zinc tolerance in *Agrostis tenuis*. Heredity 32: 309–319.

Wu, L. & J. Antonovics. 1975. Experimental ecological genetics in *Plantago*. I. Induction of leaf shoots and roots for large scale vegetative propagation and tolerance testing in *P. lanceolata*. New Phytol. 75: 277–282.

——— & ———. 1976. Experimental ecological genetics in *Plantago*. II. Lead tolerance in *Plantago lanceolata* and *Cynodon dactylon* from a roadside. Ecology 57: 205–208.

ENZYME POLYMORPHISM AND ADAPTATION IN ALPINE BUTTERFLIES[1]

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ABSTRACT

The high levels of enzyme polymorphism often detected by electrophoresis probably reflect on-going balancing selection. However, hypotheses of single gene heterosis (such as overdominance or environmental balance) do not seem adequate to account for this variation. To investigate this problem further, polymorphism was studied in Colorado butterflies of the genus *Colias*. *Colias* are easy to breed and study in the field and occupy a diverse array of habitats. Four species were studied: all were found to be highly polymorphic. Polymorphism at the α-glycerophosphate dehydrogenase locus occurred only when the species in question occupied a montane habitat; no polymorphism was seen in populations occupying alpine or lowland habitats. Three populations of *C. meadii* were examined in detail which encompass both alpine and montane habitats (crossing timberline); in one of them detailed demographic studies were carried out. In each such population, marked clines were observed in α-GPdH frequency, despite the swamping effects of migration within the population. At thirteen other loci a variety of different patterns of allele frequency are seen (some clinal, some uniform, some discontinuous), despite the fact that all loci were assayed in the same individuals. This result constitutes strong evidence of selection. There is clear evidence that particular alleles at the different loci preferentially associate together at specific locations along the cline, different assemblages occurring at different locations. A hypothesis is presented that these represent integrated metabolic phenotypes, and that the enzyme polymorphism is a multi-locus strategy to preserve that integration in a heterogeneous environment.

INTRODUCTION

In the last decade it has become abundantly clear that levels of genetic variability detected by electrophoresis are very high in animal populations. However, the evolutionary significance of this variation is not clear. The difficulty is in understanding why there is so *much* of it. Most natural populations seem to be polymorphic at around a third of their enzyme loci, and over 10% of individuals are heterozygous at a typical enzyme locus (Johnson, 1973a; Selander & Johnson, 1973; Lewontin, 1974; Harris et al., 1974; Powell, 1975). This is far more genetic variability than theory had led us to expect. The disparity from expectation is not unlike Diogenes searching for one honest man—and finding hundreds! Among population geneticists there has been a lively discussion concerning the possibility that these very high levels of polymorphism are simply "noise," with no adaptively-important differences between alleles. I will not review that controversy here, except to say that I feel the weight of the evidence favors an adaptive interpretation. Rejecting the *null* hypothesis is only the first step, however. It remains to understand the biological meaning of this unexpectedly large amount of gene variation. It is with this problem in mind that I wish to describe some aspects of the population biology of the butterfly *Colias*. Detailed study of biochemical polymorphisms in this genus suggests approaches which may help to clarify the issue.

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Experimental Approach: A Single Locus Study

To assess the adaptive significance of genetic variation is not a trivial matter. It is not enough to simply observe patterns of allele frequency which correlate with some aspect of the natural environment, as many factors other than adaptation may generate such patterns: migration, founder effect, genetic drift in small populations, linkage to other loci under selection, all may have important effects. What is required is a well-defined empirical question designed to directly contrast adaptive values. To study polymorphic variation at a single gene locus, an ideal system would involve:

1. Polymorphism for an enzyme whose physiological function is well known.
2. An organism where genetic verification of allelism is possible.
3. A quantifiable environmental factor known to significantly influence the physiological function in question.
4. Demographically characterized populations.
5. Populations living in habitats which differ in terms of the chosen environmental factor.

In such a system it is possible to examine biochemical adaptation at a single locus directly (Clarke, 1975). One may ask whether there are indeed kinetic differences between alleles, whether the functioning of the allozymes is differentially affected by the environmental factor, and whether the polymorphic patterns are consistent with the habitat differences.

Colias provides such an experimental system. Butterflies may be raised in the laboratory (on hydroponically-germinated *Vicia* the life cycle of *C. eurytheme* is about a month) and pair-wise matings made to verify the mendelian segregation of variants. By marking the wings of live individuals one may carry out mark-release-recapture studies in a straight-forward manner, and thus learn the size and genetic structure of natural populations. In Colorado a variety of species of *Colias* occur, living in quite different habitats. As an organism for the approach outlined above, this butterfly thus seems a good choice.

To examine polymorphism at a single well-characterized locus I have chosen α-glycerophosphate dehydrogenase (α-GPdH). This enzyme performs in insects much the same function that LdH does in mammals: it acts to modulate the NAD^+/NADH redox level in the cell. During insect flight this is very important physiologically, as without a means of regenerating NAD^+ prolonged flight is impossible (thus *null* mutants at this locus in *Drosophila* are flightless).

The habitat-dependence of *Colias* flight has been examined in detail by Watt (1968). These butterflies act as thermodynamic "black boxes," flying only within a very narrow range of body temperature. This critical thermal range is typically above ambient air temperature in Colorado, and the butterflies rely on solar heating to raise their body temperatures to within the bounds of the thermal flight window. This is readily observable in the field, where, when a cloud covers the sun, all *Colias* drop to the ground; when the sun reappears, the butterflies warm up within a few minutes and are flying again. Thus habitat temperature, and particularly solar flux, seems a promising choice for an environmental factor importantly affecting the functioning of the enzyme α-GPdH.

Temperature has proven a fortunate choice, as the biochemical behavior of enzyme alleles of α-GPdH in *Colias* is indeed differently affected by reaction temperature (Johnson, 1976a).

Finally, the available habitats of the Colorado *Colias* encompass many very different thermal environments. The alpine species *C. meadii* is typically found on tundra, above timberline (~12,000 ft). The montane species *C. alexandra* occurs in montane open valleys at elevations of about 9,500 ft. *Colias scudderi* lives in montane habitats of 9,000–11,000 ft in conjunction with willow (the other species are restricted to legumes). The lowland species complex *C. philodice-C. eurytheme* occurs as an agricultural pest in lowland farmland from 5,000–8,000 ft. Transitional populations occasionally occur in which populations of the lowland complex occupy montane meadows, or in which the alpine species occurs in montane habitat.

POLYMORPHISM AT THE α-GPDH LOCUS IN *COLIAS*

Polymorphism at the α-GPdH locus was examined in 18 populations over a period of five years (Johnson, 1976a). Two variant forms were detected by analysis of population samples on 7% polyacrylamide gels [there is reason to believe that additional "hidden" alleles exist which are not detected by this approach (Johnson, 1971, 1975, 1976b)]. Chemical characterization of the two allozymes indicates that the same homologous alleles occur in each of the five species examined. The two alleles segregate in crosses in a mendelian manner, and heterozygous individuals can be shown to possess three electrophoretic bands (the middle band being a heterodimer or hybrid molecule). The substrate binding kinetics of the two forms are significantly different. In particular, the faster-migrating variant enzyme binds substrate more effectively at 10°C (has a lower $S_{0.5}$) while the slower-migrating variant is more effective at 30°C. As this corresponds roughly to the thermal range of the butterfly habitat during the *Colias* flight season, this difference between the alleles is likely to be of adaptive significance.

When polymorphism for α-GPdH is compared for the 18 populations, a significant pattern is evident (Table 1, after Johnson, 1976a): all nine montane populations are quite polymorphic (heterozygosity greater than 10%), while alpine or lowland populations are far less variable. This is true within species as well as between them. Thus alpine populations of *C. meadii* are not variable at this locus, while montane populations are. The result seems quite general over the five species: for 162 alpine individuals, heterozygosity for α-GPdH averaged 6%; for 292 montane individuals, average heterozygosity was 35%; for 174 lowland agricultural individuals, average heterozygosity was 7%.

This pattern of genetic variability is consistent with what we know of the thermal nature of these habitats. While the montane valleys may get quite cold at night, they offer warmer habitats during the day than the wind-swept open tundra of the high alpine populations. It is in the colder high altitude populations that the fast allele predominates, and it is the fast allele which is the most effective binder of substrate at low temperature. Montane environments are

TABLE 1. Patterns of α-glycerophosphate dehydrogenase polymorphism in several species of *Colias*.

Species	Location (Altitude)	Habitat	Number of Individuals Analyzed	Heterozygosity of α-GPdH
C. meadii	Cumberland Pass (12,000′)	Alpine	48	0.04
	Uncompahgre Peak (12,500′)	Alpine	23	0.04
	Mesa Seco (12,200′)	Alpine	30	0.17
	Upper Cement Creek (12,000′)	Alpine	36	0.03
	Upper Queen Basin (12,100′)	Alpine	18	0
	Copper Creek (10,200′)	Montane	16	0.50
	Los Piños Pass (10,500′)	Montane	20	0.45
C. scudderi	Upper Cement Creek (11,700′)	Alpine	7	0
	Lower Cement Creek (9,800′)	Montane	21	0.24
	Taylor Park (10,500′)	Montane	32	0.17
C. alexandra	East River (9,500′)	Montane	76	0.42
	Brush Creek (9,400′)	Montane	40	0.45
C. philodice	Slate River (9,100′)	Montane	46	0.39
	Lower Cement Creek (9,400′)	Montane	22	0.27
	Hotchkiss (5,000′)	Agricultural	89	0.10
	St. Louis, Mo.	Agricultural	40	0.05
C. eurytheme	Lower Cement Creek (9,200′)	Montane	19	0.21
	Los Baños, Calif. (500′)	Agricultural	45	0.02

consistently less predictable in their thermal extremes than are alpine areas, so that the pattern as well as the range of the two habitats differ.

The general results are thus quite consistent with the hypothesis that enzyme polymorphism at the α-GPdH locus reflects adaptation to a heterogeneous thermal environment. This hypothesis makes a clear and testable prediction: when single populations occupy diverse habitats, different portions of the population should experience very different selection. Thus, for example, a number of populations of *C. meadii* are known which occur right at timberline. Portions of these populations live in alpine habitats, while other portions extend down into montane habitats. The genetic structure of one such population at Mesa Seco has been studied intensively (Watt et al., 1976), and from their mark-release-recapture studies it appears that the population is genetically continuous, with at least a few individuals passing along its entire length each generation. Thus migration within the population would be expected to render it genetically uniform—unless very strong differential selection were acting upon the two alleles.

When α-GPdH polymorphism is examined along a transect from alpine to montane areas within the Mesa Seco population, the transect is *not* uniform (Table 2). A pronounced *cline* in heterozygosity is seen: the alpine sites are essentially monomorphic for the fast allele, as observed previously, but the slow allele becomes increasingly more common as lower sites are examined. Only in the highly heterozygous lower sites are the two alleles in Hardy-Weinberg equilibrium; the higher sites show large deficiencies in the slow homozygote.

Again, this result seems quite general. When the same population was sam-

TABLE 2. α-GPdH polymorphism along a transect through the Mesa Seco population.

Year	Site Number	Altitude of Site (ft)	Number of Individuals Analyzed	Observed Frequency of α-GPdH Heterozygotes
1971	13	12,200	21	0.19
	13a	12,000	9	0.11
	12	11,500	24	0.21
	10	11,000	21	0.43
	9	10,800	5	0.80
1973	13	12,200	40	0.11
	12	11,500	40	0.21
	11	11,300	40	0.38
	10	11,000	40	0.43
	9	10,800	20	0.47

pled again two years later, an identical cline was seen. Two other timberline populations, geographically quite distant, exhibit similar alpine-montane clines in α-GPdH heterozygosity.

Thus variation at this locus is in all respects consistent with an adaptive hypothesis. One cannot, of course, rule out the possibility that selection actually is occurring on some other locus that we don't know about, and that α-GPdH is simply linked to it. This argument is something like invoking divine intervention—it can be used to explain anything, and it is never possible to falsify it. However, if linkage forms the basis for the observed α-GPdH polymorphism, it is remarkably fortunate that it has produced such a functionally suitable distribution of alleles!

VARIATION AT OTHER LOCI—THE MULTI-LOCUS PROBLEM

While a single locus approach such as described above accounts reasonably well for the genetic polymorphism seen at the α-GPdH locus, the result need not be general. Species of the genus *Colias* exhibit high levels of genetic variability at many enzyme loci (Table 3), and we have accounted for only one. What of the others?

To account for the generalized occurrence of enzyme polymorphism, one of two hypotheses is usually advanced. They are both fundamentally single-locus hypotheses. One is the hypothesis which we have used to account for the α-GPdH variation: a heterogeneous environment selecting for different alleles under different circumstances. Similarly contrasting environmental influences are known to produce a polymorphism for sickle-cell hemoglobin in man, and have been implicated in lactate dehydrogenase (LdH) polymorphism in fish and alcohol dehydrogenase (AdH) polymorphism in *Drosophila*. However, if such single-locus explanations provide the basis for most of the polymorphic enzyme variation which is being reported, then we shall have to do a great deal of work to document this fact!

An alternative hypothesis is that of molecular overdominance: hybrid enzyme molecules (formed from subunits of both parental types) are viewed as in-

TABLE 3. Observed heterozygosity in eight *Colias* populations ($N > 40$).

	C. philodice		*C. scudderi*	*C. alexandra*		*C. meadii*		
Locus	Slate River (montane)	Hotchkiss (lowland)	Cement Creek (montane)	East River (montane)	Cement Creek (montane)	Cumberland (alpine)	Mesa Seco (alpine)	Mesa Seco
α-GPdH	0.40	0.10	0	0.17	0.15	0.05	0.11	0.43
G6PdH	0	0.05	0.25	0.35	0.38	0.08	0.55	0.85
MdH-1	0.10	0	0	0.05	0	0	0	0
MdH-2	0.85	0.67	0	0.30	0.38	0.13	0.15	0.45
ME	0	0.20	0.25	0	0.08	0	0.05	0.15
FUM	0.11	0.45	0.20	0.05	0.08	0	0	0.55
PGM	0.45	0.35	0.10	0.11	0.18	0.28	0.65	0.65
TPI	0.35	0.15	0.25	0.20	0	0.15	0.05	0.05
EST-1	0	0	0	0	0	0.05	0	0
EST-2	0.65	0.50	0.15	—	—	0.20	—	0
$\overline{HET}$	0.29	0.25	0.12	0.14	0.14	0.09	0.17	0.31

trinsically more stable or kinetically superior. This functional superiority produces a direct heterosis, and because heterozygotes are always at an advantage, high levels of polymorphism result. This hypothesis has great difficulty, however, in accounting for polymorphisms at loci of monomeric enzymes without multiple subunit structures.

Thus neither of these single-locus hypotheses is particularly satisfactory. I believe that the reason for this lies less with the hypotheses than with the question they address. The key is in realizing that α-GPdH, LdH, AdH and hemoglobin are atypical enzymes. Each involves a discrete physiological function directly affected by environmentally-imposed reaction conditions (Johnson, 1973b); it is not unreasonable that a single-locus hypothesis would be satisfactory in these cases. However, this is true of few of the other loci of Table 3. Most of the polymorphic enzymes are intimately involved in intermediary metabolism, and a change in the activity of one may influence the functioning of many others. Thus a change in hexokinase, which generates glucose-6-phosphate, cannot help but effect the reactions of phosphoglucomutase, phosphoglucoisomerase, and glucose-6-phosphate dehydrogenase, all of which use glucose-6-phosphate as a substrate. It seems likely that only a multi-locus hypothesis will be able to account for variation among such loci. In this regard it is worth noting that polymorphic variation occurs primarily at regulatory (rate limiting) steps in intermediary metabolism (Johnson, 1974). This finding is very widespread and quite general (the matter is extensively reviewed in Powell, 1975). This is a pattern which one would expect only if selection were acting on *the integrated metabolic phenotype* rather than on *individual loci per se*.

One multi-locus hypothesis which seems to me very attractive is that enzyme polymorphism is selected at regulatory loci so as to buffer these reactions from environmental perturbation (Johnson, 1976c). To maintain metabolic integration

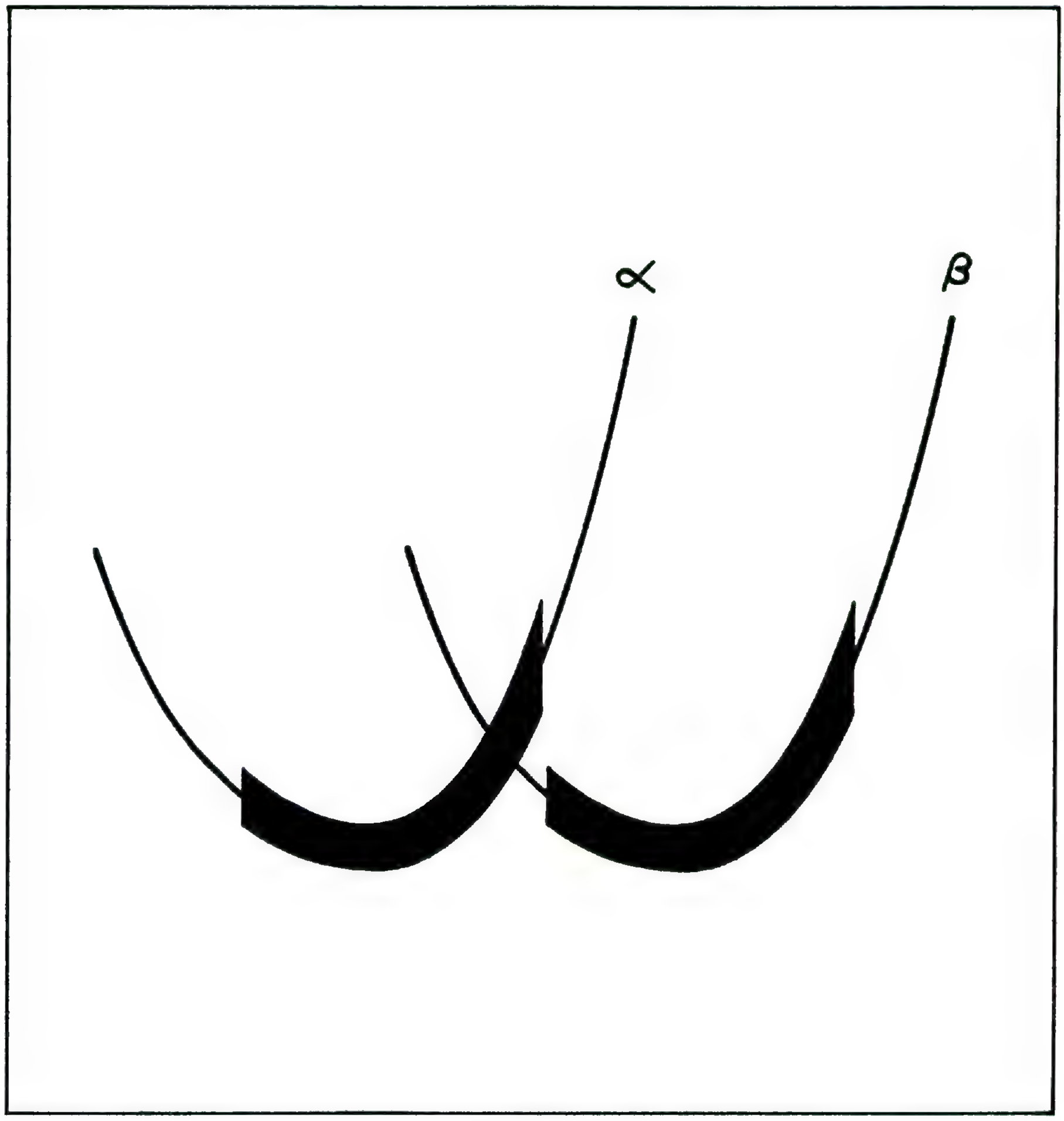

FIGURE 1. Strategies of metabolic regulation. At low temperatures form α has the lower $S_{0.5}$ (K_m) and binds most of the available substrate; both forms have allosteric sensitivity over the same range as their optimal affinity.

in a variable environment is of major evolutionary importance, as many metabolic control systems are interrelated. Yet critical reactions may respond quite differently to changes in temperature, etc. It may be of significant adaptive advantage to be able to maintain a constant relationship among critical regulatory reactions (Hochachka & Somero, 1973).

It is easy to envision molecular mechanisms which would produce such a homeostasis. Figure 1 provides one example. If the activities of two alleles respond differently to a habitat variable such as temperature (and such differences are well documented for tissue-specific isozymes), then the functional displacement with respect to temperature can buffer the coordination of metabolism from the effects of a temperature change. Any one allele of a regulatory enzyme

can exhibit a low $S_{0.5}$ (e.g. bind substrate well) only over a relatively narrow temperature range. This thermal sensitivity is an inevitable result of the requirement that regulatory enzymes be structurally flexible enough to be sensitive to allosteric "effectors" (low molecular weight molecules such as ATP whose binding acts as a metabolic signal). Over a broad temperature range a regulatory reaction cannot maintain a constant affinity for substrate and a constant binding affinity for effector molecules. As a result, it is difficult to maintain coordinate regulation with respect to other pathways catalyzed by different proteins responding differently to the change. A heterozygous individual, however, has *two* allelic forms present in each cell. In the example of Fig. 1, the α allele has the stronger binding affinity for substrate (lower $S_{0.5}$) at lower temperatures. When substrate concentrations are low, which is typically the case, only the α form will bind substrate at low temperature, and it will determine the reaction rate. Were it the only form present, the rate of binding would change at higher temperature. However, because of the functional displacement of the β allele, the β allele has the lower $S_{0.5}$ at higher temperatures. As a result, it is the β form which binds the substrate at these temperatures—and the *realized* binding affinities have not changed over the broad range of temperatures!

This model suggests that heterozygotes are not overdominant so much as conditionally hemizygous, and that it is the very difference between the alleles which produces the adaptive advantage. Polymorphism is seen as a genetic strategy for maintaining metabolic integration in the face of environmental heterogeneity.

Multiple Loci in *Colias*

The highly coordinated nature of intermediary metabolism suggests that if polymorphic alleles at regulatory enzyme loci are functionally different, then the particular allele present at one locus will importantly affect the activity of many other reactions. Thus if an individual possesses a low-temperature allele at one locus, rather than a higher-temperature form, then it makes a difference which functional forms are present at other regulatory loci. If a network of related regulatory enzymes are all optimally suited to low temperature, then one may speak of a *metabolic phenotype* adapted to these conditions. It is at this level that selection acts—on the expressed phenotype of individuals, rather than upon individual loci. Because the particular functional variant occurring at each regulatory locus influences the physiological state of the individual, *selection on metabolic phenotypes implies selection on allozymic genotypes.* To understand enzyme polymorphism, then, it will be necessary to simultaneously characterize a variety of loci in each sampled individual of a population.

Such a study is best carried out within a single population, to eliminate the possibility that differences in allele frequencies arise from demographic complications. If different loci sampled from the same individuals exhibit different patterns of allele frequency, then the result may not be attributed simply to migration or habitat selection by mobile adults.

For such a genotypic comparison, 14 loci of *C. meadii* were characterized, each individual butterfly being tested for all 14 loci. The Mesa Seco population was selected for the study, and samples were collected at each of five sites along

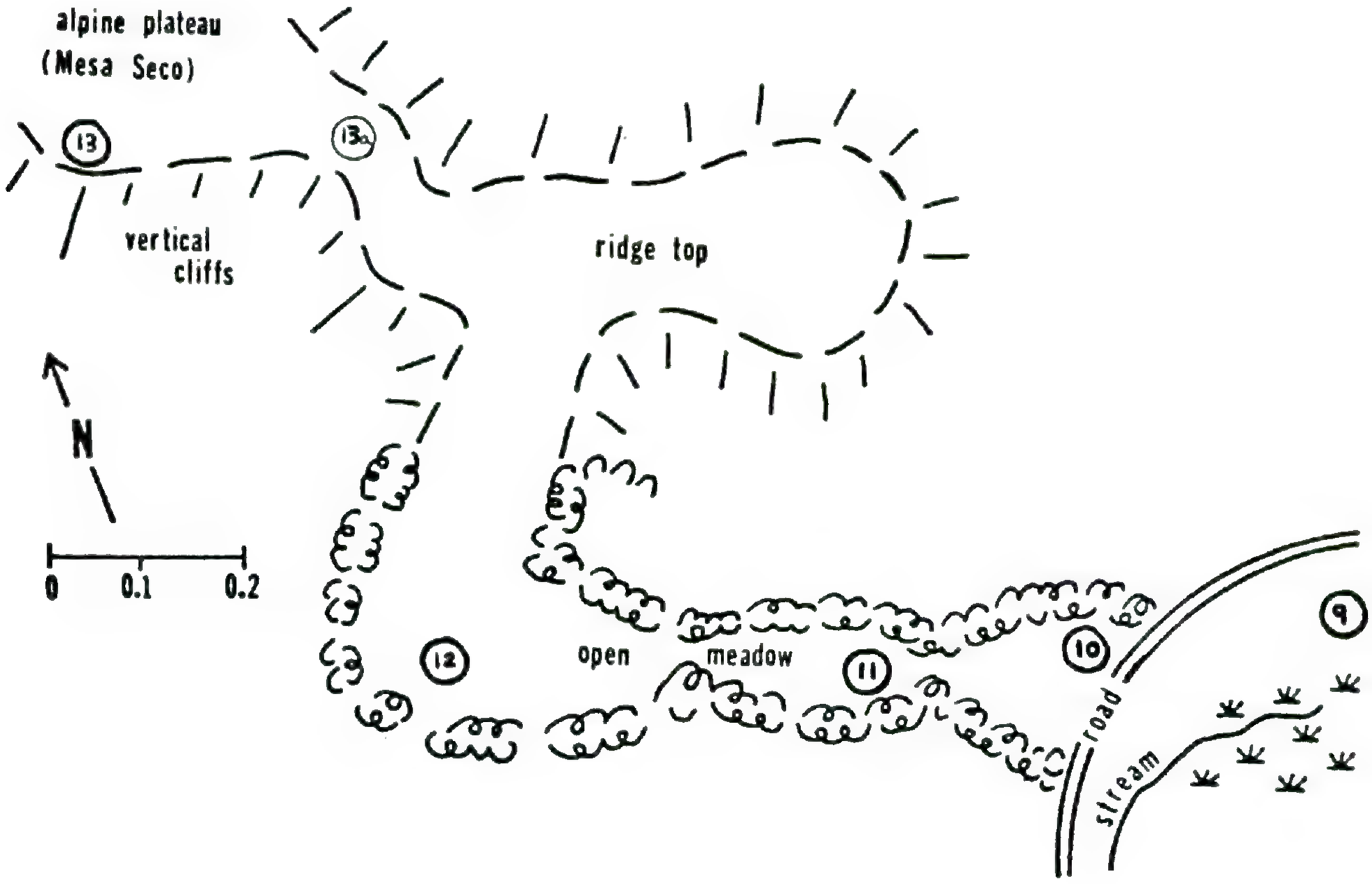

FIGURE 2. Mesa Seco population sample sites.

a transect from alpine to montane: an alpine site (#13), timberline (#12), montane forest (#11), montane forest-meadow boundary (#10), and open montane meadow (#9) (Fig. 2). The total distance traversed by the transect was about 2 miles, and the elevational difference about 2,000 ft. The population size was known from previous mark-release-recapture studies to exceed 1,000 individuals (one generation per year) and seemed to maintain approximately the same numbers from year to year. Individuals are seen to exchange between adjacent sites at a frequency of about 10%, although little or no exchange is seen between the more distal sites.

What then of the genotypes? A typical data set is presented in Table 4, that for the sample from site #9. A most startling relationship is apparent! Of 20 individuals, fully 9 appear to have highly organized genotypes: 5 individuals have identical alleles at each of 7 of the 12 loci, 4 others are identical at 6 loci. The odds that an individual would have such coordination are very low. For the first group of Table 4, the common genotype and associated allele frequencies are:

Genotype	B	—	C	—/C	A/B	A	B	—	—	—	—	B
Allele frequency	0.79	—	0.50	0.84	0.80	0.25	0.37	—	—	—	—	0.61

The joint probability that one individual will have this genotype is the product of the allele frequencies, $P = 0.02$. The probability that five individuals would possess this genotype by chance alone is only $(20/5)\ p^5q^{15}$, or 3.66×10^{-5}!

Two such commonly recurring genotypes are apparent in the sample from site #9, one involving six loci and one involving seven. The implication is very strong that they reflect selection for particular constellations of alleles.

TABLE 4. Genotypes at meadow site (#9).

Individual Number	α-GPdH	EST-1	EST-2 & 3	AK-1	AK-2	G6PdH	HK-1	HK-2	ME	PGM	FUM	MdH-1	MdH-2	TPI
1	B	—	C	B	C	A/B	A	—	B	A/C	B	—	A	B
2	B	C	C	A	C	A/B	A	—	B	B	C/D	C	A	B
3	B	A/B	C	B	C	A/B	A	—	—	B/C	C/E	C	A/B	B
4	B	—	C	A	C	A/B	A	—	B	A/B	B/D	B	A/B	B
5	B	B	C	A	C	A/B	A	—	B	B	A/B	B	A/B	B
6	B	C	D	A	C	A/B	A	B	D	B/D	C	C	B	B
7	B	A/C	D	A	C	A/B	A	B	D	A/C	C/D	A	B	A
8	B	A/B	D	A	C	A/B	A	B	D	B/C	D	C	B	A
9	B	C	D	A	C	A/B	A	B	D	B	D	—	B	C
10	B	B	C	B	C	A/B	A	B	B	B/D	D	C	B	B
11	B	A C	D	A	C	B	A	C	C	A/C	D	C	B	B
12	C	A/C	A D	B	—	B	C	B	E	B/D	A	—	A	C
13	B	—	B/D	A	C	B	A	B	C	A	C	—	B/C	B
14	B	A/C	C/D	—	—	A/B	C	B	E	B/C	D	C	B	C
15	B	A/B	—	A	C	A/B	A	B	B	A	C	—	B	—
16	—	—	C	B	C	A	A	B	C	A/C	B/C	A	B	—
17	A/B	A/B	C	A	C	A/B	A	B	B	B	D	C	B	A
18	A/B	—	B	A	C	A/B	A	B	C	C/D	B	B	B	A
19	A	—	C	B	—	A/B	A	B	C	B	D	C	B	B
20	B	C	C	B	—	A/B	A	B	D	A/D	D	C	B	B

When the other sites are examined, similar results are obtained: highly organized genotypes involving more than half the examined loci repeatedly occur at high frequency. However, these genotypic combinations are different for each site! In the face of the observed adult migration, this is a remarkable result. None of the genotypic combinations common at one site are ever observed at any other. These results are summarized in Table 5. In this table, loci where more than one genotype occurs among the group are symbolized by a dash; invariant loci (identical for the entire sample) are indicated by parentheses.

The genotypic organization seen in the results of Table 5 clearly relates to the overall metabolic phenotype, as it involves almost exclusively regulatory as opposed to nonregulatory loci. Only those reactions which significantly affect the rate of intermediary metabolism seem to be included in the organized genotypes.

I have considered α-GPdH and the esterases separately, as their functions are individually relatable to habitat factors such as temperature or secondary plant compounds. The genotypes of these loci also appear highly correlated with the localized habitat.

The unavoidable conclusion which one must draw from these results is that organized genotypes indeed exist in natural populations, apparently maintained by selection in the face of significant migration.

POLYMORPHISM AS GENETIC STRATEGY

The genotypic associations described above suggest rather strong selection. For the genotypes of site #9, the indicated fitness (expected genotypic frequency/observed) is about 0.10. This seems very strong selection, and it raises the question of how the genetic and population structure of *C. meadii* has evolved to cope with what appear to be stringent environmental constraints.

The observed properties of the *C. meadii* genetic system are: (1) It involves a very large number of small chromosomes ($2n = 62$); (2) Although each female will lay several hundred eggs during a yearly flight season, population sizes remain relatively constant (this suggests a mean zygotic fitness of the order of 0.005); (3) Mark-release-recapture studies indicate low adult mortality, suggesting that selection is primarily at the larval stage; (4) Mating appears to be panmictic within local populations; (5) Members of individual subpopulations appear to be quite sedentary: while some individuals may forage for several hundred meters, the distribution of most adult individuals appears localized to portions of the cline; (6) Unlike alpine populations of *C. meadii* studied at other localities (where there is little exchange between subpopulations), there is significant exchange between adjacent subpopulations of the Mesa Seco population.

The observed genotypic associations may be maintained in such a genetic system by at least two very different genetic strategies. One strategy is that of linkage. If the key loci are tightly linked, then the observed high linkage disequilibrium would be an inevitable result of the low recombination fraction between them (Allard, 1975). Such a hypothesis implies that the subpopulations along the cline must be genetically isolated from one another, despite migration.

TABLE 5. Genotypic combinations specifying at least ½ of examined loci.

	Environmental			Regulatory							Nonregulatory				
Site	αGPdH	EST-1	EST-2 & 3	AK-1	AK-2	G6PdH	HK-1	HK-2	ME	PGM	FUM	MdH-1	MdH-2	TPI	Freq.
13	A	—	A/—	B	( )	A/B	( )	B	B	—	—	—	B	A	0.25
	B	—	—	A	( )	B	( )	B	C	B	—	A	B	A	0.33
12	C	—	A/C	B	( )	A/B	( )	B	A	—	—	A	—	B	0.20
11	A	C	B	A	( )	A/B	( )	B	B	B/—	—	—	—	—	0.20
10	C	—	—	—	( )	( )	( )	B	C	A/—	—	—	—	—	0.35
	B	C	—	A	( )	( )	( )	B	B	—	—	—	—	B	0.20
	C	C	—	—	( )	( )	( )	B	D	—	—	—	—	—	0.15
9	B	—	C	—	( )	A/B	A	Null	B	—	—	—	A/—	B	0.25
	B	—	D	A	( )	A/B	A	B	D	—	—	—	B	—	0.20

Otherwise genotypes common in one subpopulation would appear in adjacent ones. To maintain the observed genotypic discontinuities would require strong selection.

The alternative hypothesis is that the genetic system of *C. meadii* is analogous to that of the plants on which it feeds: that it utilizes the great segregational power of its high chromosome number to produce in each generation a wide array of genotypes. From this varied assortment a small fraction survives to become adults at any given site. Different sites might then select for different genotypes. Such a genetic strategy is highly flexible, being capable of reorganizing the genotypic constitution of a local subpopulation yearly. Such a strategy would constitute ideal adaptation to an unpredictably variable local habitat.

In this respect it is worth noting that efficient food processing is of paramount importance to *Colias* larvae, and that the regulatory loci of Table 5 encompass many of the key points in physiological regulation of intermediary metabolism.

Both segregation and linkage strategies imply a heterogeneous habitat and strong selection within the Mesa Seco population. It is possible to experimentally distinguish between them by reexamining these sites in subsequent years. The population subdivision suggested by a linkage strategy predicts temporal stability: the local genotypic combination should recur from year to year. In contrast to this, a segregational strategy implies temporal as well as spatial habitat variability: the local genotypic combinations may be quite different from year to year. The data are not yet available to distinguish between these two alternatives.

It is of interest to compare the results obtained for *C. meadii* with other *Colias* species. *Colias alexandra* is known from mark-release-recapture studies to be far more mobile (a single individual may be observed to move kilometers in a day). Preliminary data comparing samples collected at two sites six miles apart (from what appears to be a genetically continuous population) reveal a single common genotype (seven loci of fourteen, at a frequency of 20%) which is the same for both sites. This presumably reflects the fact that a broad montane valley is a more uniform habitat than an alpine-to-montane transect. The result is not unlike what one might have found looking only at the alpine population of *C. meadii*. Perhaps populations of *C. alexandra* occupying a more diverse array of habitats (if such could be identified) might exhibit more than one common genotype. Alternatively, other factors may limit its distribution to these open mountain valleys.

Several populations of *C. philodice* have been examined, both agricultural populations in alfalfa fields and montane meadow populations. In two respects these populations are quite different from the *C. meadii* and *C. alexandra* populations described above: (1) They exhibit a lesser number of alleles per locus; (2) I am unable to detect any common genotypic combinations involving a significant proportion of the examined loci. Unlike the indigenous species described above, *C. philodice* is very much a weedy species and is widespread in disturbed habitats. Perhaps it avoids the specialized habitat adaptations (and specialized genotypes) of the other species by a homeostatic biochemical strategy such as discussed earlier: A small number of functionally distinct alleles may act to

buffer key regulatory reactions so as to maintain constancy over a range of environmental variability. However, such a homeostatic strategy precludes fine-tuned adaptation to subtle environmental differences. The effect is to perpetuate a particular metabolic phenotype, while preserving its coherence. In the relatively similar habitats produced by human disturbance, such a "weedy" metabolic phenotype may be optimal. It permits a coherent metabolic phenotype with less selection than is required to maintain a fully organized genotype. The trade-off here is that such a "weedy" phenotype lacks genotypic flexibility, and will not readily alter in adaptation to particular circumstances. It is an approximate solution, arrived at cheaply.

It is clear that a great deal remains to be done to understand these patterns of genetic variation. To me, the most attractive conceptual framework within which to organize the findings discussed above is to view the patterns of enzyme polymorphism seen within *Colias* butterflies as adaptive strategies, which in each case *match the flexibility of the metabolic phenotype to the heterogeneity of the environment*. The detailed information needed to evaluate this interpretation involves both biochemical study of the differential functioning of allozymes, and far more extensive surveys of natural populations.

Literature Cited

Allard, R. 1975. The mating system and microevolution. Genetics 79: 115–126.

Clarke, B. 1975. The contribution of ecological genetics to evolutionary theory: detecting the direct effects of natural selection on particular polymorphic loci. Genetics 79: 101–113.

Harris, H., D. Hopkinson & E. Robson. 1974. The incidence of rare alleles determining electrophoretic variants: Date on 43 enzyme loci in man. Ann. Hum. Genet. 37: 237–253.

Hochachka, P. & G. Somero. 1973. Strategies of Biochemical Adaptation. Saunders Co., Philadelphia, Pennsylvania.

Johnson, G. 1971. Analysis of enzyme variation in natural populations of the butterfly *Colias eurytheme*. Proc. Natl. Acad. U.S.A. 68: 997–1001.

———. 1973a. Enzyme polymorphism and biosystematics: The hypothesis of selective neutrality. Annual Rev. Ecol. Syst. 4: 93–116.

———. 1973b. The importance of substrate variability to enzyme polymorphism. Nature New Biol. 243: 151–153.

———. 1974. Enzyme polymorphism and metabolism. Science 184: 28–37.

———. 1975. Enzyme polymorphism and adaptation. Stadler Genet. Symp. 7: 91–116.

———. 1976a. Polymorphism and predictability at the α-glycerophosphate dehydrogenase locus in *Colias butterflies*: gradients in allele frequency within single populations. Biochem. Genet. 14: 403–424.

———. 1976b. Hidden alleles at the α-glycerophosphate dehydrogenase locus in *Colias* butterflies. Genetics 83: 149–167.

———. 1976c. Genetic polymorphism and enzyme function. *In* F. Ayala (editor), The Molecular Study of Biological Evolution. Sinauer Publ., Inc., Sunderland, Massachusetts.

Lewontin, R. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York.

Powell, J. 1975. Protein variation in natural populations of animals. Evol. Biol. 8: 79–119.

Selander, R. & W. Johnson. 1973. Genetic variation among vertebrate species. Annual Rev. Ecol. Syst. 4: 75–91.

Watt, W. 1968. Adaptive significance of pigment polymorphism in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. Evolution 22: 437–458.

———, F. Chew, L. Snyder, A. Watt & D. Rothschild. 1976. Population structure of Pierid butterflies. I. Numbers and movements of some montane *Colias* species. [In preparation.]

ON THE RELATIVE ADVANTAGES OF CROSS- AND SELF-FERTILIZATION[1]

Otto T. Solbrig[2]

Abstract

An optimality model based on the tradeoffs between seed set efficiency and outbreeding is presented that predicts under what conditions selfing should be favored over outcrossing. The model predicts that local density and distributional pattern, degree of environmental predictability, and adult and seed longevity are the independent variables that determine the shape of the marginal benefit curves for seed set and offspring heterogeneity. Some data supporting the model are presented derived from a study of species of the genus *Leavenworthia* (Cruciferae).

Flowering plants can reproduce in two basic ways. All species have the capacity to produce new individuals by vegetative means, such as runners, stolons, bulbs, corms, etc. Nearly all species in addition reproduce by seeds. The embryo contained in the seed is normally the result of the union of the egg cell with a gamete produced by a pollen grain from another plant and transported to the style by some pollinating agent. However, in a number of species, pollen from the same plant occasionally, or habitually, fertilizes the egg. Finally, seeds can also be produced apomictically without recourse to fertilization. From an evolutionary standpoint, the latter is better viewed not as a form of reproduction, but as a means of enlarging the parental genotype. The term vegetative propagation is therefore preferable, reserving the term reproduction for the formation of seed.

The diversity of modes of reproduction encountered in flowering plants presents a challenging problem to the evolutionist. In the present paper I review the most accepted theory and indicate what I consider to be inconsistencies with the requirements of individual Darwinian selection. I then present an alternative model and some arguments in its support. Finally I apply the model to explain the different breeding systems encountered in the mustard genus *Leavenworthia*.

Reproduction produces a number of effects. It results in the production of new individuals possessing a fraction of the parental genes. The same effect results from vegetative propagation. However, reproduction by seeds also very effectively disperses the progeny in space and/or time because seeds have the potential of being transported for long distances and going dormant for variable lengths of time to avoid unfavorable periods in the environment. The selective advantages of dispersal and dormacy have been discussed elsewhere (Crocker,

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1938; Harper, 1957; Harper et al., 1970; Gadgil, 1970; Lewis, 1973). They are a crucial aspect of the life cycle of flowering plants (Harper & White, 1971; Bradshaw, 1972). They do not explain however, the variety of breeding systems, since seeds could be (and in a few species are) produced without recourse to sexuality.

Finally reproduction results in the formation of new recombinant genotypes, an effect not duplicated by vegetative propagation or asexual production of seeds. Since the overwhelming majority of plants and animals reproduce sexually, the formation of recombinant genotypes must be selectively advantageous. What is not clear is exactly in what ways.

The Classical Hypothesis

The most commonly accepted hypothesis for explaining the diversity of breeding systems in plants was introduced by Darlington (1939, 1958, ed. 2), and further elaborated by Darlington & Mather (1949), Grant (1958, 1963), Huxley (1942), Mather (1943), and Stebbins (1950, 1957, 1958). Its seminal arguments follow closely the arguments of Muller (1932) for the evolution of sex. According to these authors there is a conflict between producing offspring that possess the superior genotypes of its parents, and species (or population) survival over time. To use the terminology of Mather (1943), there is a supposed conflict between "immediate fitness" (by which is meant individual Darwinian fitness) and "long range flexibility" (the ability to survive over a large number of generations). This conflict is supposed to arise because, according to these authors, "immediate fitness" is best attained by perpetuating the parental genotypes, which are envisioned to be superior since they have survived to reproductive age, while "long range flexibility" requires mechanisms that allow for genetic change over time. To quote Darlington (1958: 234), "Sexual reproduction survives because it profits all posterity. The opposite state of apomixis survives because it profits its own immediate progeny." Or in the words of Stebbins (1950: 170), "Sex exists . . . for any [no] other reason than its function in securing a great variety of genetic recombinations, by which the evolutionary line may adapt itself to new and varied environments."

This hypothesis makes the fundamental assumption that the fitness of a phenotype is dependent mostly on its genic endowment, that the parental genotype is always more fit in its immediate enviroment, and that the selective forces of the environment vary only slowly over space and time. Furthermore, the mechanism that it adduces for the selection of sexuality is intergroup or interdeme selection, since it is easy to show that within each population, selection should favor (if the assumptions of the hypothesis are correct) apomicts and/or selfers (Karlin & McGregor, 1974). Cogent arguments against group selection in the evolution of sex have been presented by Maynard Smith (1971) and Williams (1975). Arguments in favor of viewing the selected forces as oscillating in space and time are discussed in Solbrig & Simpson (1974) and Levin (1975) and will be elaborated further on.

AN ALTERNATIVE HYPOTHESIS

I now present an alternative cost-benefit hypothesis based on two assumptions: (1) there is an oscillating environment, and (2) all selection is individual Darwinian selection. The hypothesis balances the costs of outcrossing over self-fertilization against possible benefits from outcrossing and leads to prediction about when a plant should self and when it should increase its inclusive fitness by crossing.

We must remember that the breeding system that will be favored and ultimately selected is the one that maximizes the inclusive fitness of the parent (Hamilton, 1964). That means, the breeding system that leads to an increase of the parental genes in the following generation.

THE COSTS OF OUTCROSSING

There are two major costs associated with outcrossing. One is intrinsic to the sexual process, the second is peculiarly botanical. When an offspring is produced by self-fertilization or apomixis, it receives all its genes from one parent; when an offspring is produced by crossing, half of the offspring's genes come from one parent, the other half from the other. Some of the alleles received from the two parents are identical by descent, so that the offspring may have more than a 50% genetic similarity with each parent. Similarity rises as the number of alleles shared by the parents increases, reaching a theoretical maximum of 100% in genetically identical parents. Since fitness is the proportional contribution of genes to the next generation, each offspring produced through the sexual process contributes less to the parental fitness than offspring produced by asexual means or by selfing. Maynard Smith (1970), Williams (1975), and Williams & Mitton (1973) have termed this the "meiotic cost."

For cross-fertilization to occur in flowering plants an outside agent must carry the pollen from one plant to another. Angiosperms rely on either physical agents (wind, water) or animals (insects, birds, bats) to carry the pollen from one plant to another. This transport of pollen carries with it an energetic cost because of the mortality of pollen grains that never reach a receptive stigma (particularly high when the agent is wind or water) and because of the cost of producing structures to attract and reward animal agents (showy petals, nectar). This energetic cost results in less energy available for seed production and/or other activities compared to plants which reproduce apomictically or by selfing.

In addition, self-fertilization and especially apomixis is inherently more efficient as a method for producing embryos. Crossing requires two flowers in different plants blooming at the same time and an outside agent transporting the pollen during that period. Even under the best of circumstances some ovules remain unfertilized, and under unusual conditions (rain, cold) the failure to set seed can be significant, as is well known from silviculture and pomology.

THE BENEFITS OF OUTCROSSING

While there is general agreement regarding the cost of outcrossing, there is no consensus regarding the benefits derived from producing a genetically vari-

able progeny. There are, however, very clear benefits that can be obtained by a plant that produces variable offspring, provided the plant lives in a spatially and temporally varying environment.

The environment is treated as a constant in most discussions of breeding systems (Darlington, 1939; Stebbins, 1950; Grant, 1958), probably because most investigators have considered the physical environment. Some components of the physical environment (e.g., day length) are very predictable, but others (e.g., rainfall) are not, creating conditions under which variable progeny may be advantageous. However, interactions with other plants, herbivores, pathogens, and pollinating and seed dispersal agents also strongly influence reproductive success. This "biological environment" is very complex and is constantly changing, often at rapid rates relative to generation times of populations of plants. Furthermore, while the features of the physical environment are only marginally affected by the biological milieu (e.g., runoff patterns and precipitation can be affected by vegetation), the biological environment responds to the activities of the plant. For example, given a certain water and light regime, there is one or a fixed few optimal leaf forms that maximize photosynthesis. Once those leaf forms have been attained there will be no further response to the physical environment, nor is there a response from the environment. Similarly, a leaf predator exerts selection for the evolution of defenses against it, but as soon as those defenses begin to evolve, they become selective agents on the herbivore, favoring herbivore phenotypes that can break the plant's defenses. Also, most pathogens and herbivores have shorter generation times and larger population numbers than their hosts and can readily respond genetically to any defense the plant puts up.

In this context the immediate advantage of producing variable offspring is clear. While a plant with a leaf shape optimal for the physical environment (light and heat) may maximize its fitness by transmitting that shape to its progeny, the plant that produces offspring having exactly the same defense against a predator or pathogen risks losing all its offspring if and when the predator or pathogen breaks that defense. Therefore it will have a higher probability of producing viable offspring if each has a different kind or degree of defense against the predator and pathogen. The same argument applies for competitors. In the metaphor of Williams (1975), the chances of winning a lottery are not increased by xeroxing the same number, but by having a great variety of different numbers. See Levin (1975) for further discussion of this point.

The problem is further accentuated by the fact that plant seeds have a very limited choice of where they will grow. Consequently, the density, cover, and distance to competitors that each individual offspring seedling encounters are different from those of the parent plant and also from each other. Furthermore, they cannot avoid pathogens or predators by escape. Under these circumstances, production of only one phenotype drastically reduces the chances of success of many of the seedlings and, consequently, reflects on the fitness of the parent.

The Cost-Income Analysis

Any model of natural selection acting on a trait assumes that fitness or some component of fitness is being maximized or optimized relative to others. It also

assumes that the organism is operating within some externally (or internally) applied constraints. Fitness is clearly increased both by enlarging the seed crop and by the previous argument as a result of increased genetic heterogeneity of the offspring. The constraint is the available energy for reproduction, so that the seed crop and devices to increase the dispersal of pollen cannot be enlarged indefinitely. The problem is to find what proportional allocation of resources to these competing processes maximizes fitness.

While the costs of seed production and pollinator attraction can be measured in calories, the benefits of increased seed crops or polymorphic progeny cannot, and have to be measured in terms of relative fitness. To keep these two measures clearly separate I use the following terminology: cost = energetic input by the plant, in calories; benefit = increase in fitness; investment = cost associated in increasing fitness; marginal benefit = increase in benefit/unit of investment.

Because of insufficient information on the benefits derived from seed production and a genetically heterogeneous offspring, the arguments are based on general shapes of curves, the conclusions being based not on their exact shapes, but on their relative position to each other.

BENEFITS AND COSTS ASSOCIATED WITH OUTCROSSING

The benefit is proportional to the degree to which the progeny is unrelated to each other, that is, it will be inversely related to the coefficient of inbreeding. Assuming random breeding, the coefficient of inbreeding, F, is given by (Falconer, 1960):

$$F = 1/2\, N_e$$

where $N_e =$ the effective size of the breeding population.

The number of potential mates is correlated with the area reached by pollen (the pollen shadow) and the density of potential mates in that area. Assuming that the pollen shadow is approximately circular:

$$N_e = \pi\ r^2\ k = \alpha\ r^2$$

where $r =$ radius of the pollen shadow, and $k =$ the density of potential mates per unit surface.

The probability of mating is, however, not random as assumed, but decreases with distance as a result of the well known leptokurtic distribution of pollen (Bateman, 1951), so that:

$$PD_x = PD_o\ e^{-x/a}$$

where $PD_o =$ total pollen produced by the plant; $PD_x =$ pollen density at distance x, and $a =$ a factor that affects the shape of the pollen density distribution and depends on the kind of pollinator.

The potential benefit is then a function of plant density, the maximum diameter of the pollen shadow, and the shape of the pollen distribution curve, which depends on the total amount of pollen produced and the movements and effectiveness of pollinators.

The costs are also defined by the above equation and are the costs of pollen production (PD_a), and the costs associated in increasing the value of a, the pollinator attraction devices. When the pollen vector is a physical factor, the costs of pollinator attraction are minimal, being restricted to morphological changes in the style and the anthers. Wind or water as a pollinating agent produces very leptokurtic pollen distributions and results in high pollen mortality rates (Whitehead, 1969; Gleaves, 1973).

Additional costs associated with animal pollinator attraction are the production of showy flowers and rewards: scents, pollen, nectar, oil (Faegri & van der Pijl, 1971). Pollinators that carry pollen over large distances, such as large bees, birds, or bats, visit only flowers that offer large rewards. The amount of necessary reward is apparently positively correlated with the distance that the pollinator covers between plant mates (Opler, personal communication) although good published data are unavailable. In any case, increased gamete wastage is associated with pollination distance regardless of the pollen vector. The apparent greater efficiency of animal pollinators in relation to physical agents is compensated by the greater costs of attraction (Fig. 1). In either case, the costs of pollen production and pollinator attraction increase with the diameter of the pollen shadow, and result in fewer flowers produced and an increased pollen/ovule ratio for a given energetic commitment to reproduction.

Maximization of inclusive fitness in the present context translates into producing a pollen shadow ample enough to insure adequate genetic heterogeneity in the progeny, but not so large as to over-depress seed production by the mother plant. That is, the breeding system that maximizes fitness is the one where the reproductive energy has been invested so as to yield the greatest marginal benefit. The exact compromise between seed number and progeny heterogeneity depends on the plant's reproductive effort, the distribution and density of mates, and the life history of the plant.

Figure 2 depicts graphically how changes in patchiness and density affect the benefit derived from investments in structures that increase progeny heterogeneity. The benefit obtained for a given investment is affected by the density and the distributional pattern. This is intuitively obvious if one thinks of a plant that is wind pollinated: the lower the density of mates, and the more clumped, the greater the number of pollen grains that land in places other than receptive stigmas. Although less obvious, it is equally valid for animal pollinated plants. An efficient user of plant floral rewards should spend more time within a clump than flying from clump to clump. Furthermore, isolated plants will be undervisited. Another very important effect of a clumped distribution is that the inbreeding coefficient within a clump increases rapidly as a result of gene fixation in small populations, the so-called Wahlund effect (Wallace, 1968). This will create a threshold effect: little benefit is obtained from outbreeding until the pollen shadow is sufficiently large to cover more than one clump.

BENEFITS AND COSTS ASSOCIATED WITH SEED PRODUCTION

Figure 3 depicts the benefit derived from increased investment in seed production. I have no way of assessing the exact form of the curve, but I presume that

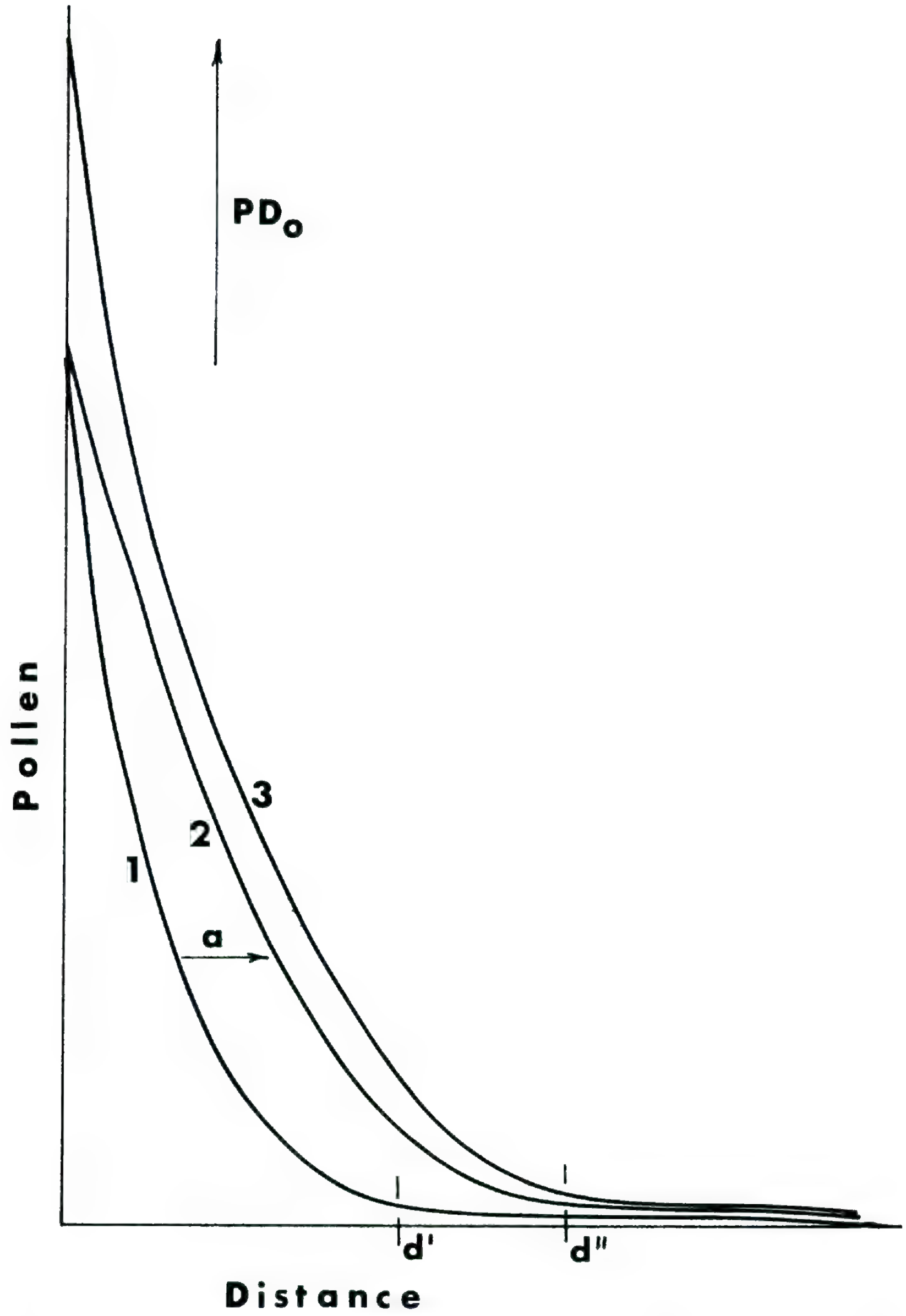

FIGURE 1. Relationship between pollen amount and distance of pollen shadow in one dimension. Curve 1 represents a random leptokurtic distribution. The effective distance of the pollen shadow is d', although some pollen will travel larger distances. To increase the effective distance to d", either the shape of the curve has to be changed by switching to a more effective but expensive pollinator (curve 2) or total pollen production has to be increased (curve 3).

it is either linear or more likely negatively exponential, since as the number of seed increases, the relative contribution that each makes to the total genetic heterogeneity decreases (assuming gene frequency remains constant). It is reasonable to suppose also that the value of each seed is in general lower for plants

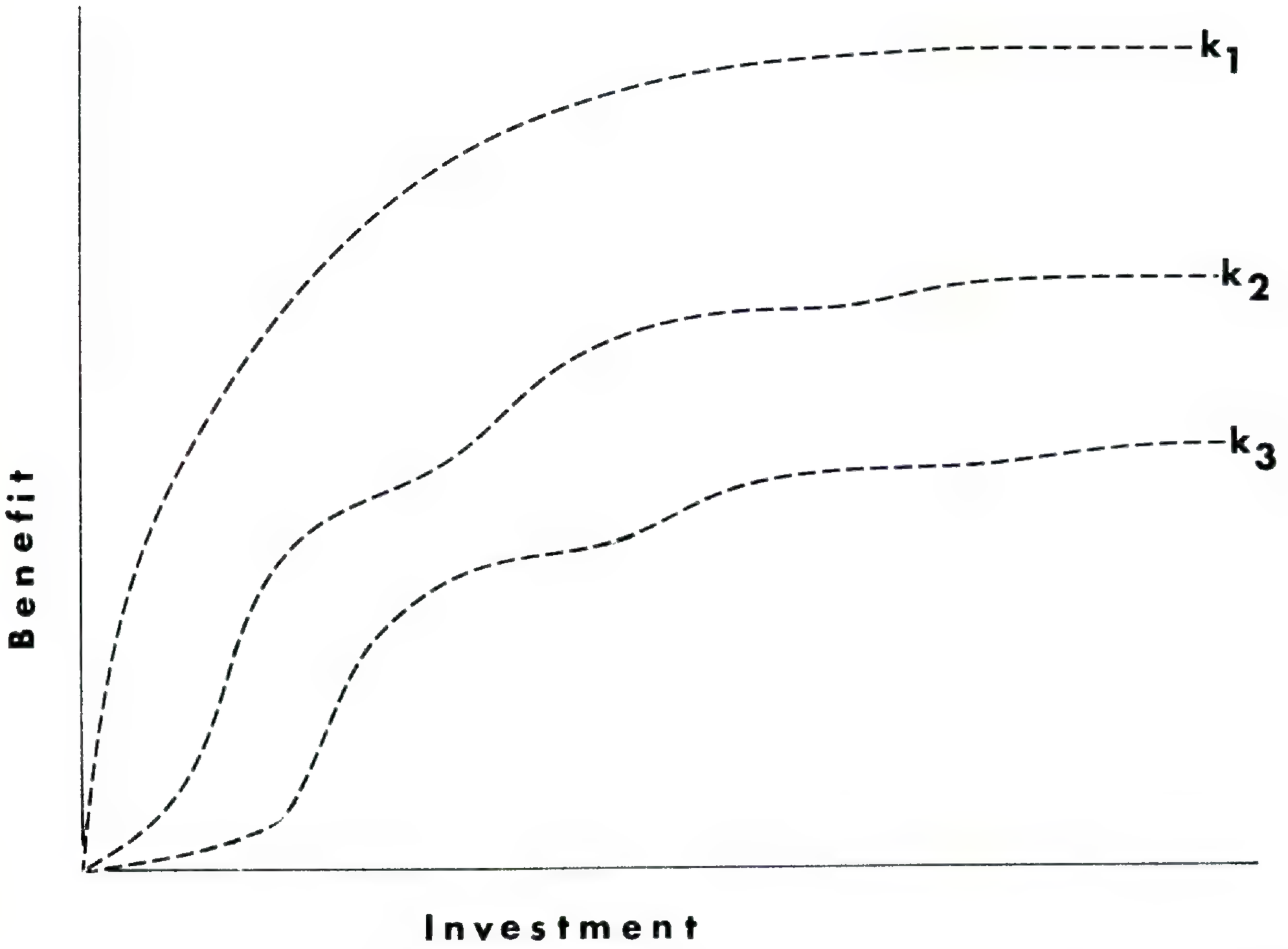

FIGURE 2. Relationship between benefit and investment in structures that increase offspring genetic heterogeneity for three levels of density and patchiness. Density of $k_1 > k_2 > k_3$; patchiness in $k_1 < k_2 < k_3$.

with long generation times, or in more rigorous terms, the value of a seed is directly correlated with its probability of germinating and growing, and is therefore correlated with the factors that control the life strategy of the species (Schaffer & Gadgil, 1975).

The costs associated with seed production are of three main kinds. First are the costs of producing the embryo and the seed coats. Seeds are usually rich in proteins and fats and have a high caloric content per gram of seed. Second are costs associated with seed dispersal (fleshy fruits, wings, spines, hairs), and finally there are the costs associated with defending seeds against predators. Caloric content is easily measured, but costs of dispersal and defense are quantified only with difficulty, and then only approximately (Harper et al., 1970; Janzen, 1969). Seed costs consequently vary from species to species, and trade-offs between investment in seed size, defense, dispersal, and seed number are to be expected (Harper et al., 1970).

THE OPTIMAL STRATEGY AND GENERAL PREDICTIONS

Figures 4A and 4B shows the marginal benefit (dB/dI) derived from different levels of investment in offspring heterogeneity and seed number for two opposite evolutionary strategies.

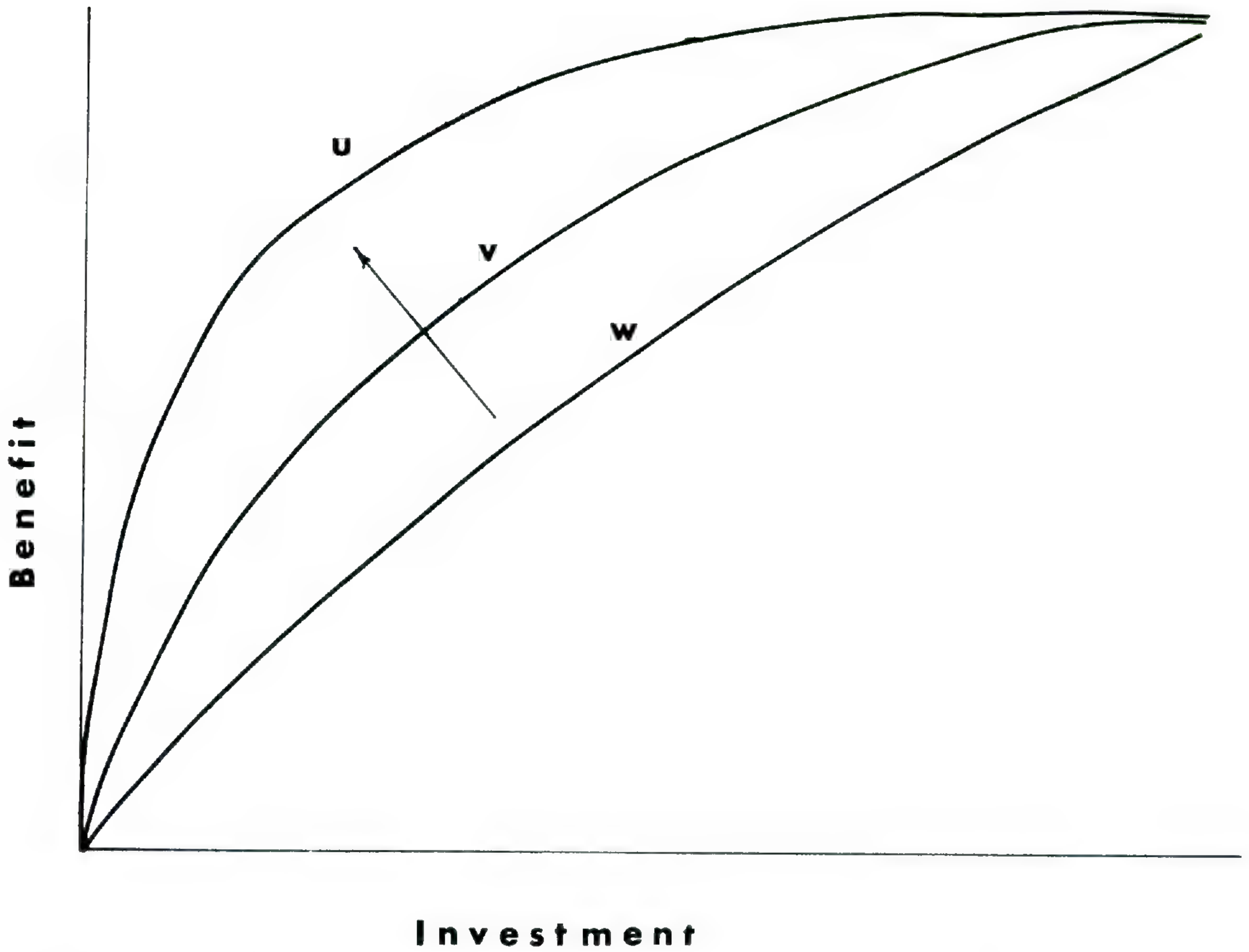

FIGURE 3. Relationship between benefit and investment in seed number for three species with different life history strategies; "r" selection increases from w to u.

Figure 4A analyzes the so-called "K" strategy (Gadgil & Solbrig, 1972). An example would be a long-lived forest tree exposed during its life-time to a variety of states of the physical environment, and subject to attack by a diversity of parasites and herbivores, as well as potential competition from many different species of plants. I further assume that such a species is more or less evenly distributed in the forest. Furthermore, because of adult longevity, replacement events should be relatively rare. A concrete example is the common beech, *Fagus grandifolia*. Under these conditions I predict that the marginal seed benefit curve will be relatively flat until a maximum is reached at relatively high investment levels (curve W, Fig. 4A). The marginal benefit curve from outcrossing should start high, reaching a maximum at relatively low levels of investment and then dropping quickly (curve K_2, Fig. 2). Although reproductive effort will tend to be low, since the plants are large and long lived, absolute investment in reproduction tends to be medium to high. Under those conditions, the analysis predicts a reasonable investment in structures to increase genetic heterogeneity through cross-fertilization, and a seed crop that should increase in direct proportion to total reproductive investment.

Figure 4B depicts the extreme opposite, "r" strategy. This is typically a fugitive species, with generations shorter than a year, exploiting a temporary resource. It grows primarily in open situations where interspecific competition is

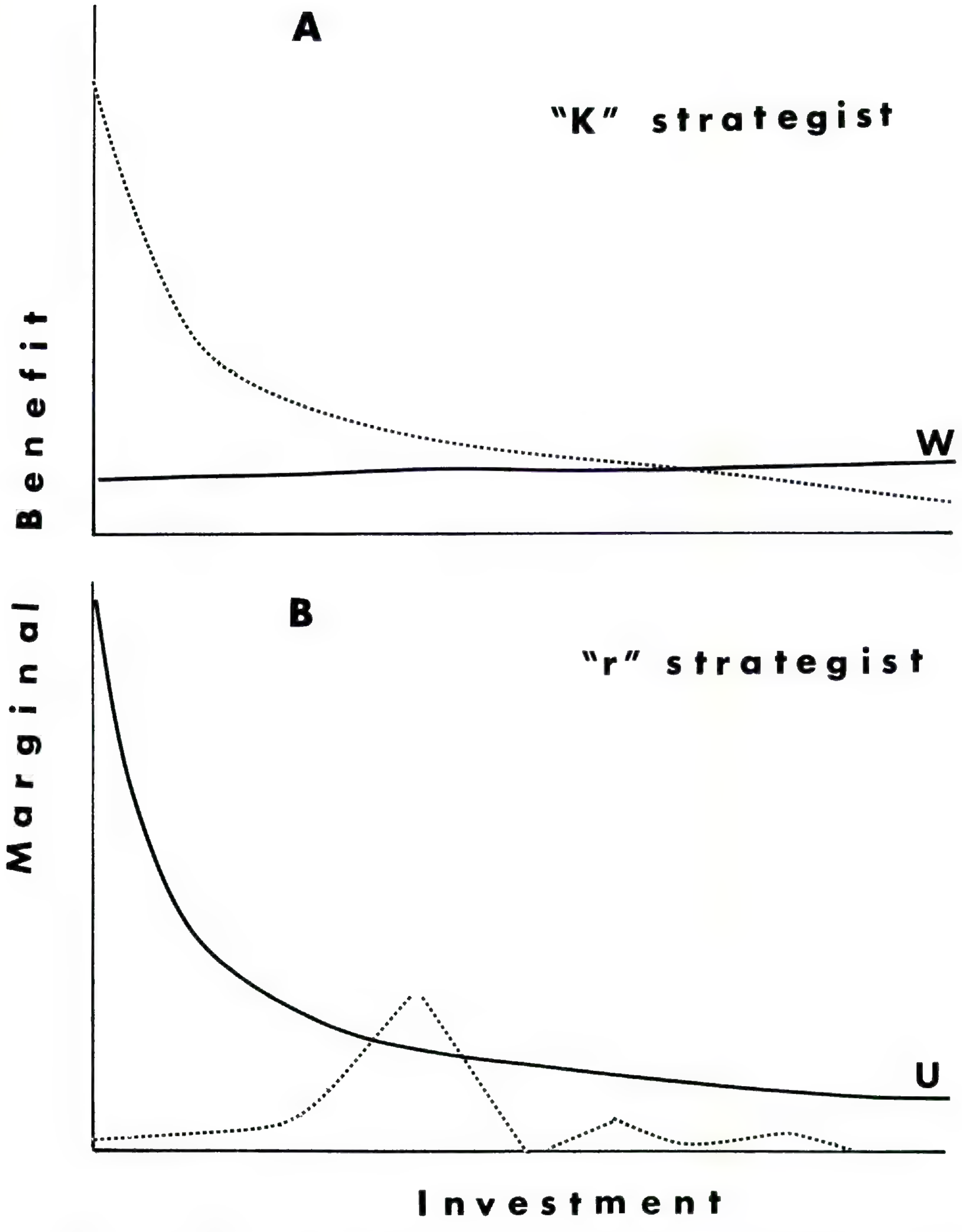

FIGURE 4. Relationship between marginal benefit and investment for an extreme "K" and "r" strategist. The marginal benefit curves obtained from Figs. 2 and 3 (tangent to total benefit) and labelled accordingly. Solid line is the value of the tangent of lines W and U from Fig. 3; dotted line is the value of the tangent line k_2 (upper) and k_3 (lower) from Fig. 2. In the "K" strategist, selfing is favored only for very low levels of investment in reproduction. However, after a certain point it is more profitable to increase the seed crop. For the "r" strategist selfing is favored for low and medium levels of investment. Further details in text.

low, and it can to some extent escape from predators and parasites due to its short life cycle and spatial unpredictability. Density will be locally high but the overall distribution will be very patchy. As a result, genetic drift (Wahlund effect and founder principle) will be important and local populations will tend to inbreed. A concrete example is the common horseweed, *Conyza canadensis*. I predict that because of the frequent replacement events and the high degree of density independent mortality, the initial marginal benefit from investment in seeds is high and decreasing thereafter (curve U, Fig. 4B). On the other hand, because of the genetic uniformity of local populations the marginal benefit of genetic heterogeneity raises slowly with investment (curve K_3, Fig. 2). Only when the pollen shadow gets large enough to encompass several subpopulations, will the benefit derived from offspring heterogeneity raise sharply. The analysis indicates that selfing is the best strategy for low and medium levels of investment in reproduction. However, for high levels of investment, there is a great marginal benefit in diverting part of the energy to the production of structures that insure outcrossing.

Between these two extremes an infinite number of combinations of seed and genetic heterogeneity marginal profit curves is possible. The exact shapes and combinations will depend on each species. However, the following general predictions can be advanced.

1. Cross-pollination should be the favored breeding system in flowering plants. In effect, selfing as a mechanism is favored only where total reproductive investment is low and where initial marginal benefit from investing in enlarging the pollen shadow is low.

2. Selfing should be more prevalent in species with small populations and clumped distributions. This is a direct consequence of the tendency of small populations to inbreed regardless of the breeding system.

3. Selfing should be more common in plants with short life cycles. This prediction follows from the increase in the marginal benefit of initial investment in seed at the expense of outcrossing and because short-lived plants tend to be smaller and can invest less energy in reproduction (although they devote a larger proportion of their available energy to reproduction).

4. Environments with low predictability will favor outbreeders, while very predictable environments will not favor them as much. This follows from the initial assumption of the model.

These predictions are testable, although a rigorous test of the model has to wait until values for the investment-benefit curves have been obtained.

THE TEST OF THE MODEL

The model can be tested in two principal ways. The first is to obtain general correlations of breeding system with pollen-shadow diameter, distribution pattern, and longevity, as well as with the appropriate measures of density and pattern, and seed number and size, in natural taxa. Stebbins (1950, 1957) and Fryxell (1957) have presented general surveys and the general correlations that they find are in agreement with the model's predictions. Additional data can be found in Baker (1965, 1972), Fukuda (1967), and Levin & Kerster (1974).

TABLE 1. Number of flowers, number of fruits, pollination efficiency, and seeds per fruit in species of *Leavenworthia*.

Population and Species	Year	No. of Plants	No. of Flowers /Plant	No. of Fruits/ Plant	Pollination Efficiency	Seeds/Fruit
exigua						
7165*	1975	50	13.0	12.2	0.94	—
7222*	1974	50	7.4	5.7	0.77	3.90
7167*	1974	50	6.6	4.8	0.73	3.70
7168*	1974	50	4.1	3.2	0.78	2.6
7168*	1975	50	5.9	5.2	0.89	—
alabamica						
7216	1974	50	10.9	8.5	0.78	6.10
7202*	1974	50	91.5	69.1	0.76	6.26
7202*	1975	50	39.1	34.6	0.89	—
crassa						
7206	1974	50	5.5	3.3	0.60	3.07
7210	1974	50	12.7	7.9	0.62	1.78
7208*	1975	50	5.1	4.1	0.80	—
stylosa						
7411	1974	50	3.7	2.0	0.54	3.0
7412	1974	50	7.3	4.2	0.56	3.3
7413	1974	50	12.8	6.7	0.52	3.8
7414	1974	50	8.5	5.1	0.60	4.3

Species marked with an asterisk (*) are self-compatible and at least in part self-pollinating.

A second way of testing the model is by searching for these relations in a specific taxon. I now present data from a field study of the genus *Leavenworthia* and compare the results with the predictions made by the model.

THE GENUS *LEAVENWORTHIA*[3]

This is a small group of winter annuals in the family Cruciferae (Rollins, 1963). The seven species of the genus can be divided into two groups each containing three diploid species, and a third group formed by a single polyploid species. One of the groups is formed by two species, *L. alabamica* and *L. crassa*, which have both self-incompatible and self-compatible populations (Rollins, 1963; Lloyd, 1965), as well as a derived self-compatible and largely self-pollinated species, *L. exigua*. These species have 11 pairs of chromosomes. The other group is formed by one self-incompatible species, *L. stylosa*, and by two self-compatible species, *L. torulosa* and *L. uniflora*. Of these, *L. uniflora* is largely self-fertilizing, but *L. torulosa* appears to be mostly outbred. These species have 15 pairs of chromosomes. All species grow on calcareous outcrops primarily in Tennessee and northern Alabama, known locally as glades.

The existence of these very closely related species with different breeding systems, and of two species with some populations that are selfers and some that are not, presents an unusual opportunity to test the model. If the model is cor-

[3] The study on *Leavenworthia* made in collaboration with R. C. Rollins.

TABLE 2. Abundance, density, frequency, and approximate size of populations in species of *Leavenworthia*.

Species and Population	Year	N	Abundance	Density	Frequency	Deviat. χ^2	Randomn. var/mean	No. of Plants/Pop.
exigua								
7165†	1975	28	88.63	30.67	21	0.26	3.939 ***	5,000
7167†	1974	50	145.89	29.18	20	218.65 **	9.603 ***	9,000
7167†	1975	49	134.09	35.61	27	67.50 *	5.343 ***	11,000
7168†	1975	39	208.33	21.21	10	4.293	15.48 ***	6,000
alabamica								
7501-a	1975	17	128.79	75.75	5	2.686	0.48	19,000
7501-b	1975	68	94.70	11.14	12	3.849	11.23 **	35,000
7501-c	1975	20	92.42	41.67	45	0.488	0.764	160,000
7502	1975	26	151.52	23.48	15	4.251	6.622 ***	58,000
7216	1975	5	75.76	15.15	20	0.668	0.5218	11,000
crassa								
7206	1974	50	196.18	28.05	14	226.79 **	14.25 ***	100,000
7206	1975	100	142.42	11.37	8	10.080**	30.84 ***	45,000
7210a	1975	18	136.36	37.88	28	33.189**	3.166 *	6,000
7210b	1975	43	279.55	123.48	44	188.36 **	4.276 ***	150,000
7208a†	1975	22	75.76	3.79	5	0.657	16.91 ***	850
7208b†	1975	52	75.76	4.55	6	1.044	15.55 ***	2,700
stylosa								
7411	1974	50	204.96	106.23	38	3882.33 **	10.38 ***	310,000
7411 (seedlings)	1974	50	490.15	146.97	30	139.46 **	9.086 ***	440,000
7411	1975	100	215.90	43.18	20	6447.36**	10.792 ***	130,000
7503	1975	43	118.94	18.94	16	99.57 **	8.44 ***	38,000

Population marked with a dagger (†) are self-compatible.
* P 0.05
** P 0.01
*** P 0.001

rect, we expect to find tradeoffs in the genetic structure of the populations, the pollination mechanisms, and in seed-set efficiency. They should be correlated with different marginal benefit curves as a result of different environmental parameters controlling the density and pattern of growth. The research design, in-depth description of the biology of these species, and discussion of the results are discussed elsewhere (Solbrig & Rollins, in press). I here present only a brief summary of the results pertinent to this discussion.

Genetic diversity was measured through the use of isoenzymes, as well as through a study of variation of three fruit characters. As predicted, populations of self-compatible and presumed selfers showed less genotypic variation, and a correspondingly high value of F (Solbrig, 1972). The analysis of the morphological variation showed a significantly higher between-family component of the variance in self-compatible populations than expected by the null hypothesis. It also was found that, regardless of the breeding system, small and more clumped populations were more inbred than larger populations. Consequently, it can be concluded that the benefits derived from outcrossing in the small and in the self-

compatible populations rise slower with investment (pollen-shadow diameter) than in the large and in the self-incompatible populations.

Self-incompatible populations are exclusively pollinated by insects, while populations of self-compatible plants are both self-pollinated and cross-pollinated by insects. However, populations of self-compatible plants invest less in pollinator attraction: flowers are smaller (Rollins, 1963; Lloyd, 1965), and they have a lower pollen/ovule ratio (Lloyd, 1965). However, seed-set efficiency, as measured by the ratio of flowers/fruits is greater in the selfers (Table 1). Both these results are expected if the model is correct.

The model further predicts that the changes in breeding system are the consequence of different marginal values of offspring heterogeneity and seed number resulting from changes in density and local distributional patterns of the populations. The density and pattern of several populations was measured (Table 2). It can be seen that there is a clear difference between selfers and outbreeders: the density and the size of the population of self-compatible (and presumed selfing) populations is significantly smaller than that of the self-incompatible populations. In these small populations (that, as was pointed out above, are genetically uniform) outbreeding increases offspring genetic heterogeneity very little. Consequently, the marginal value of producing structures to increase outbreeding is below the marginal value of producing additional seed, and it is more profitable (greater fitness) to decrease the investment in factors that promote outbreeding and transfer them to seed production by the more efficient selfing method. As seed number increases, the marginal value of each additional seed beyond a point (maximum) decreases until it becomes again profitable to invest in factors that promote outbreeding. The exact point depends on each population, and has been carefully documented by Lloyd (1965) for *L. alabamica* and *L. crassa* and by Solbrig & Rollins (in press) for *L. exigua*.

Literature Cited

Baker, H. G. 1965. Characteristics and modes of origins of weeds. Pp. 147–168, *in* H. G. Baker & G. L. Stebbins (editors), The Genetics of Colonizing Species. Academic Press, New York.

———. 1972. Seed weight in relation to environmental conditions in California. Ecology 53: 997–1010.

Bateman, A. J. 1951. Is gene dispersal normal? Heredity 4: 253–263.

Bradshaw, A. D. 1972. Some of the evolutionary consequences of being a plant. Evol. Biol. 5: 25–44.

Crocker, W. 1938. Life span of seeds. Bot. Rev. (Lancaster) 4: 235–274.

Darlington, C. D. 1939 (1958, ed. 2). The Evolution of Genetic Systems. Cambridge Univ. Press, Cambridge.

——— & K. Mather. 1949. The Elements of Genetics. George Allen & Unwin Ltd., London.

Faegri, K. & L. van der Pijl. 1971. The Principles of Pollination Ecology. Pergamon Press, New York.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. Ronald Press, New York.

Fryxell, P. A. 1957. Mode of reproduction in higher plants. Bot. Rev. (Lancaster) 23: 135–233.

Fukuda, I. 1967. The formation of subgroups by the development of inbreeding systems in a *Trillium* population. Evolution 21: 141–147.

Gadgil, M. D. 1970. Dispersal: Population consequences and evolution. Ecology 52: 253–261.

——— & O. T. SOLBRIG. 1972. The concept of "r" and "K" selection: Evidence from wild-flowers and theoretical considerations. Amer. Naturalist 106: 14–31.
GLEAVES, J. T. 1973. Gene flow mediated by wind-borne pollen. Heredity 31: 355–366.
GRANT, V. 1958. The regulation of recombination in plants. Cold Spring Harbor Symp. Quant. Biol. 23: 337–363.
———. 1963. The Origin of Adaptations. Columbia Univ. Press, New York.
HAMILTON, W. D. 1964. The genetical evolution of social behavior. I, II. J. Theor. Biol. 7: 1–16, 17–52.
HARPER, J. L. 1957. The ecological significance of dormancy and its importance in weed control. Proc. Int. Conf. Plant Protect. Hamburg 4th, pp. 415–420.
——— & J. WHITE. 1971. The dynamics of plant populations. Proc. Advanc. Stud. Inst. Dyn. Numbers Pop. Oosterbeck, 1970, pp. 41–63.
———, P. H. LOWELL & K. G. MOORE. 1970. The shapes and sizes of seeds. Annual Rev. Ecol. Syst. 1: 327–356.
HUXLEY, J. S. 1942. Evolution: The Modern Synthesis. Harper, New York.
JANZEN, D. H. 1969. Seed eater versus seed size, number, toxicity, and dispersal. Evolution 32: 1–27.
KARLIN, S. & J. MCGREGOR. 1974. Towards a theory of the evolution of modifier genes. Theor. Populat. Biol. 5: 59–103.
LEVIN, D. A. 1975. Past pressure and recombination systems in plants. Amer. Naturalist 109: 437–452.
——— & H. W. KERSTER. 1974. Gene flow in seed plants. Evol. Biol. 7: 139–220.
LEWIS, J. 1973. Longevity of crop and weed seeds: survival after 20 years in soil. Weed Res. 13: 179–191.
LLOYD, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). Contr. Gray Herb. 195: 3–134.
MATHER, K. 1943. Polygenic inheritance and natural selection. Biol. Rev. Cambridge Philos. Soc. 18: 32–64.
MAYNARD SMITH, J. 1970. Genetic polymorphism in a varied environment. Amer. Naturalist 104: 487–490.
———. 1971. What use is sex? J. Theor. Biol. 30: 319–335.
MULLER, H. J. 1932. Some genetic aspects of sex. Amer. Naturalist 66: 118–138.
ROLLINS, R. C. 1963. The evolution and systematics of *Leavenworthia*. (Cruciferae). Contr. Gray Herb. 192: 3–98.
SCHAFFER, W. M. & M. D. GADGIL. 1975. Selection for optimal life history in plants. Pp. 142–157, *in* M. L. Cody & J. M. Diamond (editors), Ecology and Evolution of Communities. Harvard Univ. Press, Cambridge, Massachusetts.
SOLBRIG, O. T. 1972. Breeding system and genetic variation in *Leavenworthia*. Evolution 26: 155–160.
——— & R. C. ROLLINS. In press. The evolution of autogamy in species of the mustard genus *Leavenworthia*. Evolution.
——— & B. B. SIMPSON. 1974. Components of regulation of a population of dandelions in Michigan. J. Ecol. 62: 473–486.
STEBBINS, G. L. 1950. Variation and Evolution in Plants. Columbia Univ. Press, New York.
———. 1957. Self-fertilization and population variability in the higher plants. Amer. Naturalist 91: 337–354.
———. 1958. Longevity, habitat, and release of genetic variability in the higher plants. Cold Spring Harbor Symp. Quant. Biol. 23: 365–378.
WALLACE, B. 1968. Topics in Population Genetics. W. W. Norton, New York.
WHITEHEAD, D. R. 1969. Wind pollination in the angiosperms: evolutionary and environmental considerations. Evolution 23: 28–35.
WILLIAMS, G. C. 1975. Sex and Evolution. Princeton Univ. Press, Princeton, New Jersey.
——— & J. B. MITTON. 1973. Why reproduce sexually? J. Theor. Biol. 39: 545–554.

INTRASPECIFIC VARIATION IN POLLEN-OVULE RATIOS AND NECTAR SECRETION—PRELIMINARY EVIDENCE OF ECOTYPIC ADAPTATION[1]

ROBERT WILLIAM CRUDEN[2]

ABSTRACT

Because pollen-ovule ratios (P/O's) reflect the predictability of pollinators in a habitat and the efficiency of pollination, large intraspecific differences in P/O's suggest differences in pollinator numbers and/or their efficiency. Plants of *Heracleum lanatum*, which is andromonoecious, from forests have larger percentages of male flowers than those outside of forests, hence a higher P/O. This difference is associated with differences in the kinds of flower visitors. I suggest the pollen removal by small bees that forage on *Heracleum* in but not outside the woods may be the selective force that accounts for the larger percentage of male flowers of woods plants.

In andromonoecious *Caesalpinia* the percentage of hermaphroditic flowers in a population ranges from 8–83%, and appears to be ecotypically adapted to levels of pollinator, i.e., butterfly, activity. Nectar secretion is continuous and is the key to successful reproduction, especially in populations with low pollinator activity. Pollination is proportional to foraging time and a function of the pollen carried. The amount of nectar in the flowers reflects pollinator activity; thus in low activity populations there will be more nectar and visits will be longer, thus increasing the likelihood of pollination. Because there are large numbers of male flowers in such populations the pollinators presumably carry more pollen, which also increases the likelihood of pollination. In populations with high pollinator activity large numbers of visits balance the shortness of individual visits. A consequence of this balanced system is that the fecundity of hermaphroditic flowers in quite dissimilar populations is equivalent. Deviations from predicted levels of seed set and fruit set are consistent with below normal levels of pollinator activity.

Nectar production in two populations of *Calliandra anomala* are quite different, with a high elevation population producing far less nectar than a lower elevation population. The low rate of nectar production in the high elevation population is undoubtedly an adaptation that forces the pollinators, i.e., hawkmoths, to visit large numbers of flowers to obtain sufficient nutrients, thus increasing fruit set and maximizing fecundity.

The breeding system and pollination biology of *Leonotis nepetaefolia* are used to explain the distribution of this African plant in Mexico, where it is a roadside weed.

The objective of this paper is to communicate initial results that suggest that two reproductive characteristics, "pollen-ovule ratios" and "nectar secretion," may have adapted ecotypically in response to differences in the kinds and levels of activity of their pollinators. Some of the data is of a preliminary nature, i.e., one year's observations, and in the future the present interpretation may require modification or reinterpretation.

FLORAL CHARACTERISTICS REVIEWED

For at least 15 years botanists have known that xenogamous flowers reflect reciprocal evolution with a pollinator class (Pijl, 1960, 1961). Floral morphology reflects the size and foraging behavior of the pollinator class. Flower color and odor reflect the visual and olfactory sensitivity of the pollinator class. For exam-

[1] The contribution of Sharon Hermann-Parker in collecting and discussing much of the data presented in this paper is greatly appreciated.

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ple, hummingbird flowers are typically red, have a tubular corolla with no "landing platform" or nectar guides, and produce no odor. In contrast bee flowers are typically blue, yellow, or white, frequently reflect ultraviolet light, may produce an odor, and have nectar guides and a "landing platform" that facilitates the landing of the insect on the flower. Recall also the rotten odor of carrion-fly pollinated flowers, e.g., *Stapelia*.

To the morphological characteristics we can add the constituents of nectar, e.g., amino acids and lipids, the timing of nectar secretion, and the quantity of nectar produced. For example, the nectars of butterfly flowers contain relatively large quantities of amino acids whereas the nectars of bee flowers contain relatively small quantities of amino acids (Baker & Baker, 1973, 1975). Bees have alternative sources of amino acids. Not surprisingly, carrion-fly flower nectars contain extremely high quantities of amino acids which help to simulate the usual microhabitat of the flies (Baker & Baker, 1973). With respect to the timing of nectar production, in *Penstemon kunthii* G. Don secretion begins approximately 1½ hours prior to the first visits by hummingbirds and ceases at approximately the same time the hummingbirds cease activity (Cruden et al., 1976). Further, the volumes and quantities of sugar in nectars reflect the energetic demands of the flowers' pollinators (Table 6). Thus it seems that virtually every aspect of the structure and function of xenogamous flowers is the result of coevolution with their pollinators.

Characteristics of autogamous flowers reflect their breeding system. In comparing xenogamous and autogamous flowers Ornduff (1969) calls attention to a number of characteristics that facilitate self-pollination, e.g., introrse anthers that are adjacent to the stigma, as well as other characteristics that typify autogamous plants, e.g., small flowers and relatively low numbers of pollen grains. Such differences occur between species (Arroyo, 1973; Baker, 1967) and within species (Lloyd, 1965). As systematists we need to be aware that comparisons of floral characters may lead to erroneous phylogenetic conclusions if we unwittingly compare the products of convergent evolution. For example, in *Limnanthes* the utilization of floral characters led to taxonomic conclusions contrary to those generally accepted (Ornduff & Crovello, 1968). However, using vegetative characteristics the species fell nicely into two subgenera that represent two phyletic lines. In each phyletic line there is a series of species which include xenogamous species at one extreme and autogamous species at the other (Ornduff & Crovello, 1968).

A characteristic sometimes overlooked by systematists is the number of flowers that are open at a given time. Low numbers of open flowers maximize outcrossing in all plants and maximize effective pollinations in self-incompatible plants. Levin et al. (1971) suggested that the amount of legitimate pollen transfer decreases with each flower visited and that six to ten flowers is the maximum number of flowers that can be visited before all pollinations become geitonogamous. In *Calliandra*, fruit set ranged from 10–14% in those species and populations with few flowers open at a time compared to 1–5% in populations with many flowers open at a time (Cruden, 1976a).

TABLE 1. Relationship between pollen-ovule ratios, breeding systems, and successional stage.

Pollen-Ovule Ratio $\bar{x}$ of $\bar{x}$'s ± S.E.	Number of Populations	Breeding System	Successional Stage	Number of Populations	Pollen-Ovule Ratio $\bar{x}$ of $\bar{x}$'s ± S.E.
27.7 ± 3.1	7	Obligate autogamy			
			Highly disturbed	23	135.6 ± 23.5
168.5 ± 22.1	20	Facultative autogamy			
			Early successional	24	588.7 ± 100.3
796.6 ± 87.7	38	Facultative xenogamy			
			Late successional Pollinators unreliable	23	1877.4 ± 423.6
5859.2 ± 936.5	25	Xenogamy	Late successional Pollinators reliable	15	7251.5 ± 1396.1

POLLEN-OVULE RATIOS

A pollen-ovule ratio (P/O) is the ratio of pollen grains produced per ovule. The details of calculating P/O's, a list of the species studied, etc. are presented elsewhere (Cruden, 1976b). P/O's range from 2.7 in cleistogamous flowers to over 1,000,000 in wind pollinated flowers. Using an outcrossing index, which was based on flower size, homogamy vs. dichogamy, and the relative position of stigmas and anthers, 96 populations representing 80 species were placed into one of several groups. Each group has a characteristic breeding system and P/O (Table 1). Obligately autogamous species have no apparent adaptations for outcrossing. Facultatively autogamous plants do have adaptations that facilitate outcrossing, but all those studied set full complements of seeds when pollinators were excluded. Many species produce nectar and are visited by potential pollinators, for example, *Verbena bracteata* Lag. & Rodr. and *Salvia tiliaefolia* Vahl, but outcrossing in this group probably is not the rule. Facultatively xenogamous plants are adapted for outcrossing, but all those studied were self-compatible and many were autogamous. Others required a pollinator. If dichogamous, they are protogynous, a system that favors outcrossing but does not preclude selfing. A good example of a facultatively autogamous species is *Mirabilis nyctaginea* (Michx.) MacMill., whose flowers open in late afternoon and are visited and pollinated by bees. They remain open during the night and are

TABLE 2. Breeding system characteristics and fecundity in *Hedeoma hispida*.

Population	1	2	3	4
Breeding System	Obligate Autogamy	Facultative Autogamy	Facultative Autogamy	Facultative Xenogamy
Length of flower/calyx	1	1.2	1.5	1.8
Width of corolla (mm)	1–1.5	2–3	2.5–3.5	3.4
Pollen-ovule ratio	39	64.2	109.9	244.7
Pollination (%)	100	100	98	43
Seed set (%)	98	97	93	73
Fecundity (%)	98	97	91	31

pollinated by moths; if unpollinated, they remain open and are visited again by bees in the morning, and if still unpollinated, they may self on closing (Cruden, 1973). Xenogamous species are outcrossers. Many, if not most, are self-incompatible. If self-compatible, they are probably strongly protandrous or more rarely functionally dioecious, as are many umbells (Cruden & Hermann-Parker, unpublished). Most species produce nectar and all those studied require a pollinator.

Prior to establishing the breeding systems of the species studied, each population was classified as to habitat or successional stage. It is not surprising that autogamous species are characteristic of highly disturbed habitats and that as succession occurs there is a switch to xenogamy. The data are consistent with accepted dogma, namely, that autogamy is adaptive in disturbed habitats because replication of successful genotypes assures continued success in such habitats. What is exciting and suprising is the ability to identify plants growing in advanced successional stages whose adaptations facilitate outcrossing but are able to self-pollinate or be selfed. If pollinators are unreliable, there is an obvious advantage in being self-compatible. The xenogamous plants in pollinator-unreliable habitats are, for the most part, early spring species, self-compatible, and protogynous. Xenogamous plants in habitats with reliable pollinators tend to be obligate outcrossers and suffer reduced fecundity if their pollinator activity is reduced (Cruden, 1972). The point is that breeding systems, including P/O's, are highly adapted to the ecological conditions in which the plant normally grows and in particular reflect the predictability of pollinators in the habitat.

Variation within species mirrors the variation that exists between species. Such differences were studied most thoroughly in *Hedeoma hispida* Pursh (Table 2). There is a significant increase in the P/O with the potential for outcrossing as measured by corolla exsertion and flower diameter. The increase in potential for outcrossing is correlated with a decrease in seed set in the autogamous populations, and there is a sharp decrease in both fruit set and seed set in the facultatively xenogamous population. The latter population was in a disturbed roadside park which lacked appropriate pollinators. It is clear that in disturbed habitats the facultatively xenogamous genotype would be at a selective disadvantage, with respect to reproductive success, compared to the autogamous genotypes. This illustrates the adaptive nature of autogamy in highly disturbed habitats, habitats in which pollinators may be absent or in low numbers.

Variation in the P/O's of Andromonoecious Species

A small number of plants produce inflorescences which contain both hermaphroditic and male flowers. Such inflorescences are typical of most Umbelliferae and some taxa in other families, e.g., various genera in Mimosaceae and Caesalpinaceae, and the commercially important *Mangifera indica L.* In four of five umbelliferous species studied to date the ratio of male to hermaphrodite flowers is constant. In *Heracleum lanatum* Michx. the ratio varies with habitat (Fig. 1). The number of hermaphrodite flowers in the primary umbells of "interior" plants is significantly different from those of plants in "openings" and outside the forest ($t = 3.94$; $p < .001$). Likewise the number of hermaphrodite flowers in the lateral umbells increases significantly from interior to outside populations ($F = 16.11$; $p_{df = 2,\ 69} < .001$). The array of flower visitors to inflorescences in "interior" populations is markedly different from that to "openings" and "outside" populations. The "interior" plants are visited heavily by small bees and small flies. The "outside" and "opening" plants are visited heavily by large flies and infrequently by small bees. The small bees may constitute a possible selective pressure if they remove significant amounts of pollen. In *Viola*, a small but significant decrease in the number of viable pollen grains was correlated with a significant decrease in fecundity (Cruden, 1976b). I suggest that increased numbers of male flowers may be a selective response to pollen loss from foraging bees. This hypothesis remains to be tested.

In *Caesalpinia* a number of reproductive parameters vary from population to population (Table 3), including percentage of hermaphroditic flowers, number of pollen grains per anther, and number of ovules. These three parameters contribute to the pollen-ovule ratio of a population and the P/O may vary markedly from population to population. The percentage of hermaphroditic flowers changes from year to year but probably varies around some genetically controlled mean. In other words, the variation we see probably has both a genetic and environmental component as is apparently the case in *Mangifera indica* (Free, 1970).

Data collected in 1975 (Table 4) suggest a positive correlation between the number of hermaphroditic flowers and butterfly activity ($r = .952$; $p = .05$). In those populations with low numbers of hermaphroditic flowers seed set is roughly proportional to pollinator activity. In the Mazatlán population seed set is low in spite of high pollinator activity. In general, fruit set is high when seed set is low.

A brief summary of pollinator behavior and the pollination biology of *Caesalpinia* will be helpful in understanding these results and the notions based on the results. The primary pollinators are species of *Battus* and *Papilio* (Papilionidae) which flutter before flowers while removing nectar. Pollen is carried on the underside of the wings and the wing area to stigmatic surface ratio is approximately 19,000:1, essentially equal to the bat-wing to stigma ratio of 18,000:1 reported for *Bauhinia pauletia* (Heithaus et al., 1974).

Although the ratio of male flowers is correlated with butterfly activity, the critical element in *Caesalpinia*'s reproductive biology is the continuous secre-

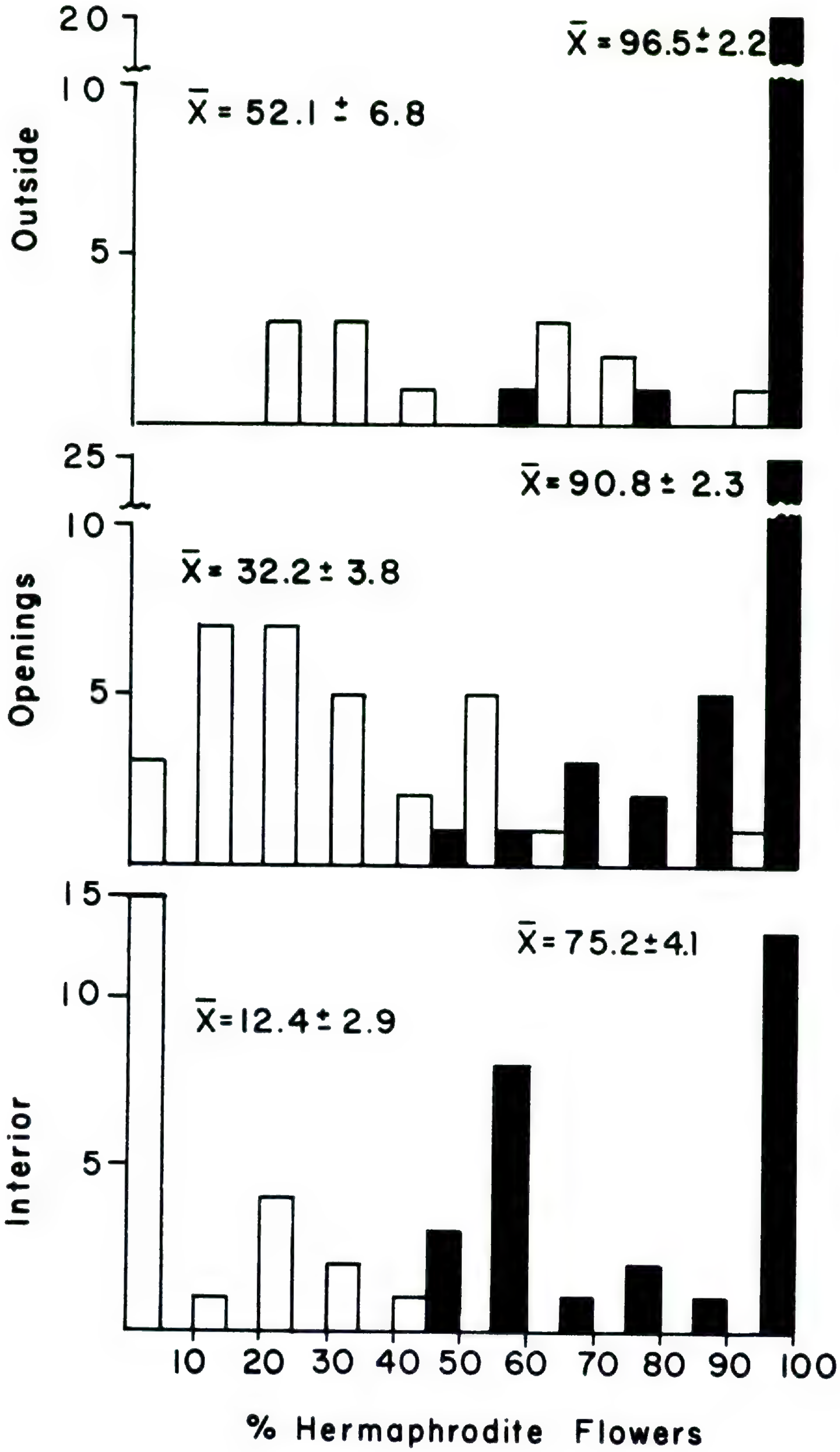
Outside
20
10
5
X̄ = 52.1 ± 6.8
X̄ = 96.5 ± 2.2
Opening
25
10
5
X̄ = 32.2 ± 3.8
X̄ = 90.8 ± 2.3
Interior
15
10
5
X̄ = 12.4 ± 2.9
X̄ = 75.2 ± 4.1
10 20 30 40 50 60 70 80 90 100
% Hermaphrodite Flowers

TABLE 3. Reproductive characteristics in four populations of *Caesalpinia pulcherrima* in Mexico.

	Year	Mazatlán	Colima NE	Miramar	Audiencia
Hermaphrodite flowers (%)	1974	83	23	14	—
	1975	88	33	27	11
Pollen grains per anther		721 ± 19	551 ± 53	606 ± 34	694 ± 23
Ovules per ovary		9.9 ± 0.2	6.2 ± 0.1	7.3 ± 0.1	6.7 ± 0.1
Pollen-ovule ratio	1975	877	3863	—	—
	1975	827	2693	3074	9416

tion of nectar. In other species for which we have data (N = 12) nectar accumulation reaches some maximum, and nectar secretion stops and resumes only if nectar is removed from the flower. The pattern of nectar secretion in *Caesalpinia* is thus atypical. The position and amount of nectar in male and hermaphroditic flowers also play an important role in the reproductive process. The rate of nectar secretion in hermaphroditic flowers is two to three times that in male flowers. The nectar in the male flowers is hidden deep in the floral tube which is a modified petal. The position and amount of nectar in male flowers serve to bring butterflies in contact with the anthers and little more. Nectar rises in the floral tube of the hermaphroditic flowers allowing a butterfly to hover higher thus increasing the likelihood of a butterfly's wing striking the stigma which is lateral to and higher than the anthers.

As the rate of nectar extraction is proportional to the amount of nectar in the flower, the butterflies spend more time at the hermaphroditic flowers. The greater the accumulation of nectar the greater the likelihood of successful pollen transfer.

The amount of nectar available to an individual butterfly is a function of the number of butterflies relative to the number of open flowers. If pollinator activity is high, little nectar is available and visits are short, but many flowers are visited. This should maximize fruit set and tend to result in lower seed set. Conversely, where pollinator activity is low, relatively large amounts of nectar will accumulate in the flowers and when a flower is visited, the butterfly will require more time to extract the nectar. Because fewer flowers are visited, fruit set should be lower but seed set will be high because of the increased pollen transfer that results from spending longer times at each flower. These predictions are consistent with our observations (Table 5).

These observations and assumptions suggest a testable hypothesis. First, if the percentage of male flowers in a population is a selective response to levels of pollinator activity, then large numbers of male flowers should act to increase

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FIGURE 1. Shift in the frequency of hermaphroditic flowers from shaded to open habitats in *Heracleum lanatum*. Solid bar = terminal umbell; Open bar = lateral umbells. $\bar{x} \pm$ S.E. are given for each group. Interior = below canopy; Openings = areas along streams where canopy is not closed; Outside = edge of forest where influence of canopy is minimal.

TABLE 4. Relationship between pollinator activity, percent hermaphrodite flowers, and seed set in populations of *Caesalpinia pulcherrima* in Mexico in 1975.

	Mazatlán	Colima NE	Miramar	Audiencia
Number pollinator visits/hr. to each flower (0900–1230 hrs.)	16.50	1.43	0.79	0.21
Hermaphrodite flowers (%)	88	33	27	11
Seed set (%)	59 ± 10[a]	84 ± 2	75 ± 3	69 ± 3

[a] 1974 data, 1975 seed crop destroyed by hurricane Olivia.

the pollen load carried by individual butterflies such that the total amount of pollen carried by the pollinator population is roughly equivalent in all populations. Second, because nectar secretion is continuous, relatively large amounts of nectar will accumulate in the flowers of "high male" populations. The likelihood of pollination will be increased because of large pollen loads and "long" visits at each flower. In "low male" populations equivalent levels of pollination may occur because the flowers are visited repeatedly. In essence, a stigma, regardless of the percentage of male flowers in the population, should be exposed to an equivalent number of pollen grains. This leads to the prediction that equivalent percentages of hermaphroditic flowers should set fruit in populations with quite different levels of pollinator activity, assuming the level of pollinator activity is equivalent to long-term levels of activity to which the flower population is adapted. Below normal levels of pollinator activity should result in decreased fruit set and increased seed set.

With respect to hermaphroditic flowers, fecundities in four populations (Table 5) were not equivalent. The fecundities of the Mazatlán and Audiencia populations were equivalent as were those of Colima NE and Miramar. The fecundities of the latter two populations are approximately 35% of the Mazatlán and Audiencia populations. The lower fecundities are the result of low fruit set. The low fruit set and the high seed set in these populations are consistent with the theoretical expectations for fecundity in populations with less than average pollinator activity.

TABLE 5. Relationship between percent hermaphrodite flowers, seed set, and fruit set in populations of *Caesalpinia pulcherrima* in Mexico.

	Year	Mazatlán	Colima NE	Miramar	Audiencia
Hermaphrodite flowers (%)	1974	83	23	14	—
	1975	88	33	27	11
Pollen-Ovule ratio	1974	871	3863	—	—
	1975	827	2693	3074	9416
Seed set (%)	1974	59 ± 10	68 ± 4	—	—
	1975	—	84 ± 2	75 ± 3	69 ± 3
Fruit set hermaphrodite/all flowers (%)	1974	15/13	10/2.3	—	—
	1975	—	5/1.7	4/1	14/1.5

TABLE 6. Mean nectar volumes and sugar concentrations in various flower classes.

Flower Class	Number of Species	Volume (μl)	Range	Sugar (mgm)	Range
Hawkmoth	20	31.67	3.83 –213.3	5.41	0.62 –26.3
Hummingbird	13	11.32	3.49 – 25.32	2.39	1.02 – 4.84
Butterfly	7	1.76	0.078– 3.96	0.43	0.024– 0.80
Bee	8	2.18	0.14 – 7.39	0.76	0.05 – 3.05

The equivalent fecundities in the Mazatlán and Audiencia populations are consistent with the model, i.e., that fecundities in hermaphroditic flowers should be equivalent in populations with quite different percentages of male flowers. For the moment, at least, I suggest that the number of male flowers in a population is an ecotypic response to levels of pollinator activity. However, it is the continuous nectar production that is the key to the system. Without continuous nectar production, fecundity in "high male" populations would be low due to short visits at each flower and reduced pollen transfer. Continuous nectar production through its effect on pollinator activity, especially in "high male" populations, effectively increases the likelihood of pollination.

NECTAR

Our work in nectar production (Cruden, Hermann-Parker & Peterson, 1976) has centered primarily on the differences between various flower classes. Our data substantiate the predictions of Heinrich & Raven (1972) and the field observations of numerous investigators that flowers pollinated by high energy requiring animals produce significantly more nectar than flowers pollinated by low energy requiring organisms (Table 6). Further, our studies show that the timing of nectar production is correlated with the activity cycle of the pollinator, as in *Penstemon kunthii* and in *Caesalpinia pulcherrima* Sw. In the latter species, nectar secretion starts approximately 30 minutes prior to the arrival of the first butterflies and nearly one hour before maximum butterfly activity.

Intraplant variation in nectar production plays an important role in the reproductive success of several plants we have studied, *Caesalpinia* being one example. For several decades (Epling & Lewis, 1952) botanists have known that bumblebees forage on *Delphinium* inflorescences from bottom to top. Steve Peterson, a graduate student at the University of Colorado, has found that the lower "pistillate" flowers produce twice as much nectar as the upper "staminate" flowers. The pattern of pollinator activity, undoubtedly a response to the amounts of nectar in the flowers, maximizes outcrossing in this self-compatible group.

Deceit has been implicated in the pollination of several species. Such may be the case in hummingbird pollinated *Cuphea llavea* Lav. & Lex, whose flowers mature acropetally as in *Delphinium*. The nectar of the "staminate" flowers contains 2.50 ± .68 mgm sugar compared to .53 ± .19 mgm sugar in the "pistillate" flowers. The low amounts of nectar in the "pistillate" flowers and lack of nectar in approximately one-half of the flowers sampled suggest that nectar secretion

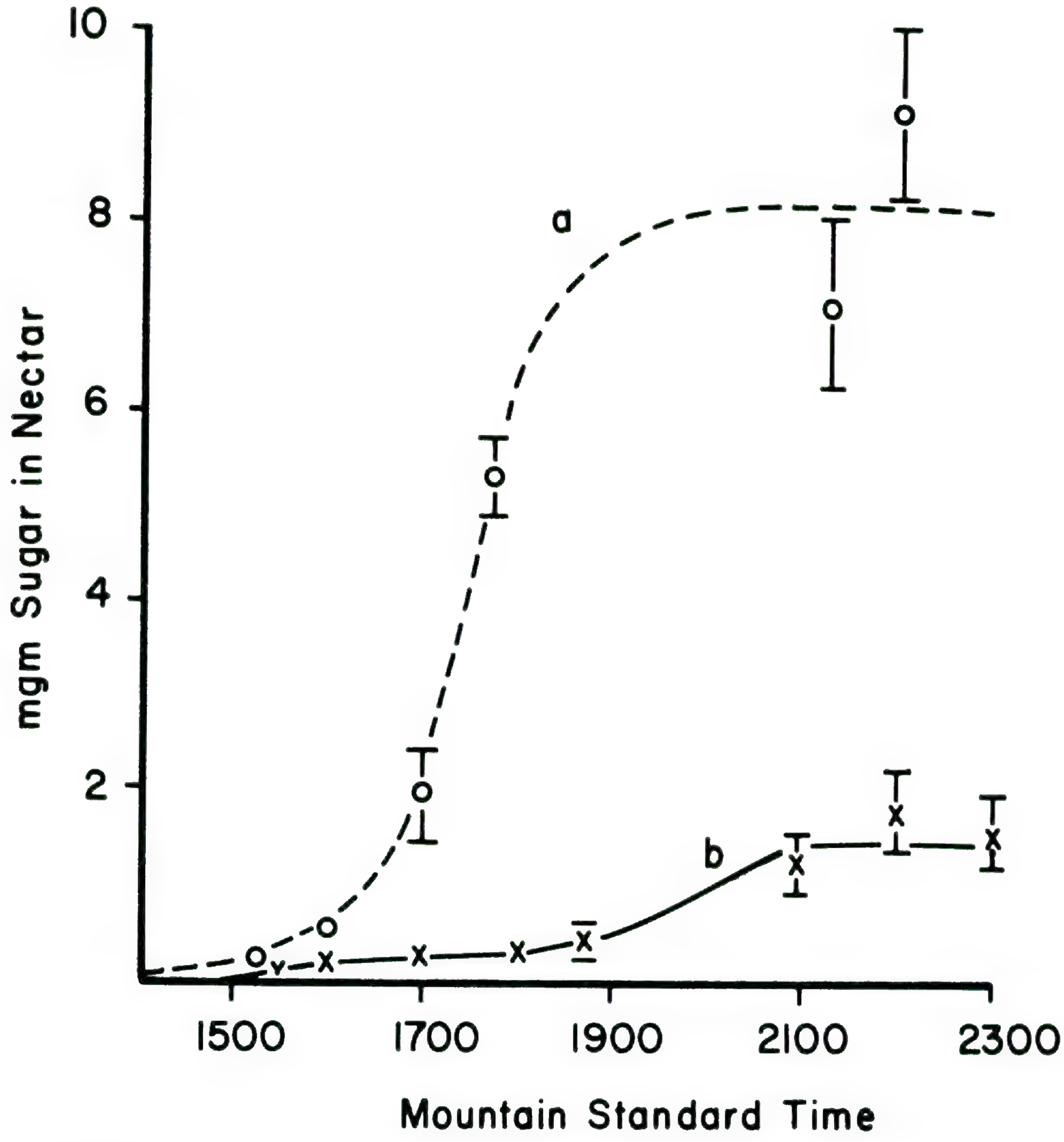

FIGURE 2. Nectar production in a 2,350 m population (solid line) and a 2,050 m population (broken line) of *Calliandra anomala*.

ceases after the "staminate" phase. By receiving a relatively large reward from the "staminate" flowers and occasional rewards from the "pistillate" flowers, the hummingbirds are not discouraged from visiting both staminate and pistillate flowers.

Our work on interpopulational differences in nectar production is somewhat meager, but the data generate tantalizing notions. We have studied nectar production in two populations of *Calliandra anomala* (Kunth) Macbr. (Fig. 2). The low elevation population is directly adjacent to the toll road from Mexico to Cuernavaca, probably resulting in severely reduced pollinator activity due to the constant movement of traffic. We studied a population at the same elevation a few kilometers away with respect to seed and fruit set (Table 7). Nectar

TABLE 7. Comparison of pollinator activity and reproductive success in two populations of *Calliandra anomala*.

	Low Elevation (2,100 m)	High Elevation (2,350 m)
Flowers visited (%)	42	78/49[a]
Flowers pollinated (%)	25	18/11
Fruit set (%)	12	1
Seed set (%)	70	42
Fecundity	0.084	0.004

[a] Two days' data.

production in this population is undoubtedly similar to that of the toll road population. Low nectar production in the high elevation population was correlated with larger numbers of visited flowers and lower numbers of pollinated flowers than the lower elevation population. Fecundity is clearly different.

At high elevations hawkmoths are active for brief periods of time. I have suggested elsewhere (Cruden, 1976a; Cruden et al., 1976) that low nectar production is an adaptation that maximizes fruit set by forcing the pollinator to visit large numbers of flowers. Fecundity is maximized because the first visit to a flower results in more seed set than subsequent visits. The adaptiveness of low nectar production in the high elevation *Calliandra* population is consistent with other hawkmoth pollinated species at high elevations. High elevation species regularly produce less than 1 mgm of sugar per flower ($\bar{X} = .99$, $N = 5$) compared to a mean of 5.66 mgm for 15 hawkmoth pollinated species studied at elevations below 2,400 m.

A second example of interpopulational differences in nectar production stimulates ideas as to the steps involved in the evolution of hummingbird flowers. Throughout most of its range the flowers of *Cuphea aequipetala* Cav. are small and probably produce small amounts of nectar as does a population at 3,000 m in the state of Morelos ($.48 \pm .05$ mgm sugar). This is consistent with the amount of sugar in the nectars of other bee pollinated flowers. Infrequently, at relatively low elevations (2,100–2,300 m) we found populations of large-flowered plants. In one of these the flowers produced large volumes of nectar containing $3.05 \pm .50$ mgm of sugar, which is more sugar than most hummingbird nectar contains.

TABLE 8. Characteristics of Mexican *Leonotis nepetaefolia* populations.

	Low	Mid
Elevational range	1–1,000 m	1,000–2,200 m
Flower length	19– 25 mm	30– 43 mm
Volume of nectar	5.62 ± 0.27 µl	11.54 ± 0.74 µl
Amount of sugar	0.90 ± 0.05 mgm	1.91 ± 0.13 mgm
Pollen-Ovule ratio	2,653	12,575
Probable pollinators	Hummingbirds, small bees	Large bees
Breeding system	Facultatively xenogamous	Xenogamous
Seed set in greenhouse	95%	63%
Fruit set in greenhouse	100%	95%

Both in Oaxaca and Jalisco, hummingbirds, as well as bees, foraged for nectar on *C. aequipetala*. Increased flower size and the concomitant increase in nectar production is a logical first step in the shift from bee to hummingbird pollination.

EVOLUTION OF THE WEED *LEONOTIS NEPETAEFOLIA*

Our interest in nectar production and P/O's first interested us in *L. nepetaefolia* R. Br., an African species widely distributed in the New World. Our nectar measurements called attention to significant differences in flower size between low and mid elevation populations (Table 8). The small-flowered form, which occurs along both coasts of the New World, is similar to specimens collected along the west coast of Africa. The earliest specimens I have examined date from the second decade of the 1800's. In the New World the large-flowered form is found almost exclusively in the central highlands of Mexico, primarily between 1,500 and 2,000 m. These plants are virtually identical with collections from around Nairobi, Kenya, in east central Africa. A third form of *L. nepetaefolia* occurs in eastern Africa and has undoubtedly given rise to the weedy populations in India, Southeast Asia, Indonesia, Australia, etc.

The small-flowered form is a good example of a facultatively xenogamous plant. It is visited and undoubtedly pollinated by hummingbirds and small bees. In the greenhouse, with bees excluded, fecundity was 98%. In contrast, the large-flowered form, which is pollinated by sunbirds in Kenya (Gill & Wolf, 1975), is visited illegitimately by hummingbirds which take nectar from the flowers by slitting the corolla or depressing it from above. The P/O (2,653:1) of the small-flowered form is consistent with its being facultatively xenogamous. The high P/O of the large-flowered race suggests xenogamy and is somewhat inconsistent with the relatively high level of fecundity (60%) in plants growing in the greenhouse. I suggest that the large-flowered form is recently arrived in the New World and that the evolution of an autogamous race may be occurring. The earliest specimens I have examined were collected in the 1930's. It is not unreasonable to suppose that the large-flowered form is an escape from horticulture and certainly any tendency toward autogamy would be rapidly selected. Indeed, if the African plants are not autogamous, escape from horticulture would be dependent on a mutation that permitted some selfing.

LITERATURE CITED

ARROYO, M. T. K. 1973. Chiasma frequency evidence on the evolution of autogamy in *Limnanthes floccosa* (Limnanthaceae). Evolution 27: 679–688.

BAKER, H. G. 1967. The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. Taxon 16: 293–300.

——— & I. BAKER. 1973. Some anthecological aspects of the evolution of nectar-producing flowers, particularly amino acid production in nectar. Pp. 243–264, *in* V. H. Heywood (editor), Taxonomy and Ecology, Academic Press, New York.

——— & ———. 1975. Studies of nectar-constitution and pollinator-plant coevolution. Pp. 100–140, *in* L. E. Gilbert & P. H. Raven (editors), Coevolution of Animals and Plants. University of Texas Press, Austin.

CRUDEN, R. W. 1972. Pollinators in high elevation ecosystems: The relative effectiveness of birds and bees. Science 176: 1439–1440.

———. 1973. Reproductive biology of weedy and cultivated *Mirabilis* (Nyctaginaceae). Amer. J. Bot. 60: 802–809.

———. 1976a. Fecundity as a function of nectar production and pollen-ovule ratios. Pp. 171–178, *in* J. Burley (editor), Variation, Breeding and Conservation of Tropical Forest Trees. Academic Press, New York.

———. 1976b. Pollen-ovule ratios: A conservative indicator of breeding systems in flowering plants. Evolution (in press).

———, S. M. Hermann-Parker & S. Peterson. 1976. Patterns of nectar production and plant-pollinator coevolution. [In preparation].

———, S. Kinsman, R. E. Stockhouse II & Y. B. Linhart. 1976. Pollination, fecundity, and the distribution of moth flowered plants. Biotropica 8: 204–210.

Epling, C. & H. Lewis. 1952. Increase of the adaptive range of the genus *Delphinium*. Evolution 6: 253–267.

Free, J. B. 1970. Insect Pollination of Crops. Academic Press, New York.

Gill, F. B. & L. L. Wolf. 1975. Economics of feeding territoriality in the Golden-Winged Sunbird. Ecology 56: 333–345.

Heinrich, B. & P. H. Raven. 1972. Energetics and pollination biology. Science 176: 597–602.

Heithaus, E. R., P. A. Opler & H. G. Baker. 1974. Bat activity and pollination of *Bauhinia pauletia*: Plant-pollinator coevolution. Ecology 55: 412–419.

Levin, D. A., H. W. Kerster & M. Niedzlek. 1971. Pollinator flight directionality and its effect on pollen flow. Evolution 25: 113–118.

Lloyd, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). Contr. Gray Herb. 195: 3–133.

Ornduff, R. 1969. Reproductive biology in relation to systematics. Taxon 18: 121–133.

——— & T. J. Crovello. 1968. Numerical taxonomy of Limnanthaceae. Amer. J. Bot. 55: 173–182.

Pijl, L. van der. 1960. Ecological aspects of flower evolution. I. Phyletic Evolution. Evolution 14: 403–416.

———. 1961. Ecological aspects of flower evolution. II. Zoophilous flower classes. Evolution 15: 44–59.

ON SELECTIVE PRESSURES AND ENERGY ALLOCATION IN POPULATIONS OF *RANUNCULUS REPENS* L., *R. BULBOSUS* L. AND *R. ACRIS* L.[1]

José Sarukhán[2]

Abstract

Selective pressures seen through patterns of mortality in plant populations seem to occur mostly in two fashions: (a) between germination and establishment for sexually reproducing species, and (b) at any moment, independently of age, during the adult life of vegetatively reproducing species. Studies on the mortality processes in three *Ranunculus* species in Welsh coastal grasslands showed that they are nonsynchronous for the three sympatric, closely related species. Studies on the distribution of biomass in vegetative and sexual structures showed a clear relation between rates of mortality and rates of individual growth, mortality being negligible at times of low individual growth. Comparisons of crude reproductive effort alone defined the vegetatively reproducing species (*R. repens*) as a "K-selected" species, while the exclusively or mostly sexually reproducing *R. bulbosus* and *R. acris* were shown to be "r-selected" species. However, when biomass expenditure on propagule production, whether by sexual or vegetative means is compared, all three species appeared to invest almost identical proportions of their biomass in structures aimed at maintaining population numbers at equilibrium. The possible significance of these patterns of energy expenditure in the three buttercups is discussed briefly.

There have recently been frequent references in the ecological literature to the imbalance between demographic information on animals and plants (Sarukhán & Harper, 1973; Harper & White, 1974, for example). Pleas for an increase on actuarial studies about plant populations have followed remarks on the lack of plant demographic studies, and indeed an answer is being given to those pleas. A clearly increasing number of direct actuarial studies (Hartshorn, 1972; Hawthorn, 1973; Hett & Loucks, 1971; Kays & Harper, 1974; Sarukhán & Harper, 1973; Sarukhán, 1974; Sarukhán & Gadgil, 1974; Sharitz, 1970; Symonides, 1974; Thomas & Dale, 1974; Werner, 1975); or the reinterpretation of data with potential actuarial information (Harper, 1967; Harper & White, 1974; Sagar & Mortimer, in press) have sprung from the initial thrust of the early pioneer works of Tamm (1956), Rabotnov (1950, 1956) and Sagar (1959), and are starting to form a body of information on plant ecology of a unique nature.

However, as soon as information coming from actuarial studies on plants began to be analyzed and interpreted in a common context with colateral information on various aspects of plant population biology, such as patterns of thinning in natural and sown populations, the plastic responses of plants to environmental stresses, mechanisms of density dependent mortality, etc., it became clear

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Ann. Missouri Bot. Gard. 63: 290–308. 1976.

that an uncritical adoption of methods and concepts of animal demography to the study of plant populations is not wise.

A discussion on some of the fundamental differences in the growth forms of higher plants and higher animals that have a profound bearing on their population behavior can be consulted in Harper & White (1974), so only a passing reference to this aspect will be made here.

Plant plasticity is perhaps the single most important factor determining the behavioral uniqueness of plant individuals and populations. Numerous examples have been cited concerning the enormous differences on the demographic contribution of individual plants of the same species under different environmental stresses [e.g., *Agrostemma githago* L. can vary the production of capsule numbers in a proportion of 6 to 1 due to increasing plant densities (Harper & Gajic, 1961)]. Even-aged populations develop extremely skewed distributions of individual size due to increased densities, especially when care has been taken in replenishing exhausted resources in the system (e.g., adding nutrients as density increases). Therefore, age may be a poor parameter for describing populational changes. For example, Werner (1975) has shown that *size* of plants of *Dipsacus fullonum* L. and *not age* is a much better element for making predictive statements concerning the death, survival and flowering of teasels.

There are numerous examples in forest literature showing a clearly marked lack of correlation between trunk diameter (d.b.h.) and chronological age, so interpretations of "population structure" based on the distribution of diameters often becomes confusing if not meaningless. However, data gathered on nearly 200 individuals of a pure stand of *Pinus hartwegii* Lindl. in Central Mexico have shown a remarkable positive correlation between age and d.b.h. (Sarukhán & Dirzo, in preparation).

Mortality Processes

Although abundant data exists on mortality in plant populations, mostly man-managed populations, most of it is ancillary to demographic approaches and it is often difficult to interpret in terms of general patterns or processes of selective pressures.

One way of looking at selective pressures in plant populations is by the analysis of some of the available data on life-tables of plant species. Of the 3 types of survivorship curves first described by Deevey (1947), types I and III imply the existence of selective pressures concentrated on particular stages of the life histories of the organisms.

It is of particular interest that all the data available for species dependent on sexual reproduction show survivorship curves of Deevey type III, where selective pressures are stronger in the earlier (seedling) phases of the life cycle, while populations which maintain their numbers by vegetative reproduction show in most cases a clear exponential rate of mortality from the very first moments of the "birth" of the daughter plant (Sarukhán & Harper, 1973); this type of survivorship is often obtained when one observes populations of mature plants. It has been suggested elsewhere (Sarukhán & Harper, 1973) that the great mortality risks involved at the seedling stages in sexually reproducing species, may be more

the result of the genetic load of unfit genotypes than the problems for metabolic adjustment between the stages of the food dependent seedling and the self-sufficient established plant.

The safety of the vegetative reproduction as against the risky sexual reproduction in plants is illustrated with the probabilities of survival of seedlings and daughter plants of *Ranunculus repens* to the year next to their "birth." These probabilities are 0.12 for a seedling and 0.77 for a daughter plant. Another species, *R. acris* also showing both modes of reproduction has probability values of survival to one year of 0.12 for seedlings and of 0.71 for daughter plants.

Mortality processes in mature plants have been described in fair detail and a general principle on the way plant populations are thinned under pressures of density-dependent mortality seems to emerge from abundant data. This principle refers to the way individual plants of a population react plastically to environmental stresses so that a situation of a yield ceiling is achieved, a ceiling which is fixed by a slope very near to the $-\frac{3}{2}$ power (Yoda et al., 1963; White & Harper, 1970; White, 1975) when log mean yield per plant is plotted against log density of survivors.

However, although a reasonably general description of mortality processes has been reached, the explanation of the mechanisms by which selective pressures act on natural populations still lies greatly in obscurity.

Analysis of the mortality processes in *Ranunculus repens* have shown that life expectancy of individuals, for example, decreased significantly with increasing density of the populations (Sarukhán & Harper, 1973). It was also clear that the highest mortality rates per week were obtained not in the unfavorable phases of the physical environment but were coincidental with the active growth of the plants.

Data from single species populations under experimental conditions also show clearly a higher mortality risk of individuals at the moment of maximum growth (Langer, 1956), and the same has been observed in natural populations of *Plantago rugelii* Decne. and *P. major* L. in Canada (Hawthorn, 1973).

Moreover, an analysis of the patterns of growth and mortality in *R. repens* shows rather clearly that the latter increases sharply when growth rates are highest and is negligible when growth is not occurring or is minimal.

Not only the detailed analysis of mortality patterns within a plant population can be revealing of the source and strength of selective pressures, but also the general mode in which these pressures incide on the life cycle of plants.

A comparison of the occurence of mortality pressures among the three closely related sympatric species *Ranunclus repens*, *R. bulbosus*, and *R. acris* has shown striking differences in the manner in which mortality acts in regard to time of the year and stages in life cycles.

The major periods of mortality in mature populations of the three species of *Ranunculus* occurred during spring and early summer but were not synchronous. The process of mortality started earliest in *R. bulbosus*; it was followed by *R. acris* and finally by *R. repens*. A prereproductive peak of mortality occurred in all the species. It was earlier in *R. bulbosus* than in *R. acris*, *R. repens* being

clearly the latest. A postreproductive peak of mortality also was obvious, and was more conspicuous than the prereproductive peak in *R. repens* and *R. acris*.

A conspicuous trough in mortality occurred in the three species coincidental to the time at which maximum flowering was taking place.

The seasonal pattern of mortality of the newly recruited population showed even greater differences between the 3 species: (a) Mortality of newly recruited vegetative propagules in *R. repens* follows closely that of the mature individuals while populations of newly emerged seedlings of *R. bulbosus* and *R. acris* constituted a distinct period of mortality in the population. (b) Times of occurrence of seedling mortality vary from early to late spring for *R. acris* and *R. repens*, respectively, and to late autumn for *R. bulbosus*.

The high risk of death involved in maintaining or replacing population numbers by seeds, reflect the experimental nature of the sexual propagules, and it is here where selection against unfit genotypes must occur.

The ramets or vegetative propagules represent tested genotypes which can expand clonally or contract depending on the current year's environmental conditions, but they always seem to be represented in the populations and ready to expand when conditions are amenable for a given genotype.

Direct evidence on the selective nature of mortality forces is nonexistent in the few available plant demographic studies since genotypes have not been studied and their performance or fitness tested. However, indirect evidence suggests that mortality acts on certain individuals of the population, particularly weak, nonaggressive plants, and selective pressures like competition or grazing certainly do affect the amount of progeny left by different genets in a population.

Energy Allocation

The characteristics of living organisms cannot be defined in space alone—a herbarium specimen of a buttercup defines its form only at one point in time. The individual plant or animal has a life cycle with a temporal pattern of growth and development that is repeated over the generations. This recurring cycle is a fundamental property of living as opposed to purely physical systems and is the element which confers much of the interest in demographic studies.

In the course of its life cycle an organism accumulates materials and energy available in its environment and disposes of them in the production of different organs. Cody (1966) and MacArthur & Wilson (1967) have pointed out that natural selection will operate on the form in which the resources are allocated by the organism in such a way as to maximize its contribution to future generations. Selection acts on an "adaptive surface" in which what is "spent" on one structure cannot be spent on another. Morphology of organisms can therefore be thought of as the selective compromise of resource allocation to different organs which results in a successful strategy for a species, and in comparing species it is highly relevant to enquire how they differ in such allocation and strategy. Allocation of energy to reproduction as opposed to structures which may confer aggressiveness (height, extensive roots, etc.) or resistance to predators (spines, toxins, etc.) is often of prime interest.

Theoretical ecologists have recently laid much stress on the concept of "r" and "K" strategies, recognizing that the selective forces acting on species that spend most of their life as colonizers are different from those that suffer density stress in stable communities. Colonizing species ("r" strategists) are envisaged as the result of selection for high fecundity; such species allocate large proportions of their available resources to reproduction and little to structures that allow them to become better established in their community or to avoid predation; therefore, high fecundity is often linked to low aggressiveness. In contrast, species of closer or more stable habitats ("K" strategists) may have improved their long term survival by devoting a great proportion of their resources to structures which confer advantages to individuals in the struggle for existence, although at the cost of reduced fecundity. The study by Gadgil & Solbrig (1972) on "r" and "K" selection in plants is an outstanding example of this approach.

Ogden (1968) has compared a few plant species with respect to the proportion of their annual assimilation that is devoted to seed production and showed that, in general, annuals had high values (30–40%) and perennials, particularly those reproducing vegetatively, had low values (5–10%).

This "reproductive effort" of the species should ideally be determined by knowing the proportion of the total energy of the plant as starting capital (i.e., as an embryo) plus its gross assimilation that is invested in propagules (Harper & Ogden, 1970); but because there are obvious technical difficulties in assessing gross assimilation, approximate but more practical forms have been used in the estimation of reproductive efficiency. The "harvest index" of crop plants (e.g., Donald, 1962; Stern & Beech, 1965) estimates the reproductive effort of species as the proportion of the total weight or biomass of plants at maturity that is allocated to propagules. Harper & Ogden (1970) have used the calorific energy allocated to reproduction for the description of the strategic distribution of the resources of a plant.

The data on plant growth and dry matter allocation which follows was obtained to complete a comparative demographic study of three *Ranunculus* species. It was intended to provide the necessary information to understand inter- and intraspecific interactions of the three species, as well as to throw more light on the interpretation of the acturial data gathered for the three species.

Plants of *Ranunculus repens*, *R. bulbosus*, and *R. acris* growing under natural conditions in the University College of North Wales experimental field at Aber, Gwynedd, were used for the study during the growing season of 1969. The biology of the species and the characteristics of the site have been dealt with elsewhere (Harper, 1957; Sarukhán & Harper, 1973).

Two contrasting sites of collection for each species were selected, based on the degree of grazing of the site. Thus, for each species site I represents the more intensely and site II the more lightly grazed condition. Twenty mature plants of each species were sampled at random within each site at the following dates in 1969: 20 April, 17 May, 29 May, 16 June, 23 June, 30 June, 6 July, 16 July, and 1 August. This period covered most of the growing cycle of the three species.

Adequate extraction of root material from the soil presents a major obstacle to studies of productivity and dry-matter allocation in plants. Bearing in mind

that it is an impossible task to extract whole root systems from the soil the following procedure was adopted to obtain a common basis for comparison of the energy allocated to roots in the three species of buttercups. A special metallic cylinder was placed carefully around a buttercup plant and a soil core of constant volume (5.3 cm in diameter, 9 cm deep = 200 ml) was obtained. The metallic sampler had sharp edges to facilitate cutting through the superficial root mat and to reduce compaction of the soil when sampling. Two metallic wings 9 cm from the edge of the sampler ensured that samples of soil exactly 9 cm deep were obtained.

Once collected, the soil cores containing the plants were placed separately in labelled polythene bags and transported to the laboratory. The cores were soaked in water in separate containers and then placed under a gentle jet of water to remove the soil particles; the plant material was sorted by hand and the maximum possible amount of roots recovered; this operation was carried out over a very fine sieve that retained loose roots. Although it was possible to train the eye to distinguish the roots of the three species of buttercups from those of other species present, a considerable proportion of the very fine rootlets that became loose could not be identified with certainty and therefore was not included with the rest of the plant material. Each plant was partitioned into several components:

R. repens: 1. Rosette leaves with petioles. 2. Stolon leaves with petioles. 3. Roots of the main rosette. 4. Stolons (sometimes including rootlets in the nodes). 5. Stems (the remainder of the vegetative aerial part of the plant after having removed petioles, roots and stolons). 6. Flowers. 7. Fruits (achenes and the fruiting head).

R. bulbosus: 1, 3, 5, 6, 7, 8. Corm.

R. acris: 1, 3, 5, 6, 7. Stems in *R. bulbosus* and *R. acris* included floral stems.

The data presented refers to the standing crop or biomass of the plants at the moment of harvest. As plants of the three species, particularly *R. repens* and *R. bulbosus* undergo more or less complete physiological renewal every year, it is probable that their biomass in the initial phases of growth did not differ greatly from their net dry matter production. However, some dry matter may have been lost through grazing and tissue decay in the later samplings. Ogden (1968, 1970), for example, estimated that in high density stands of *Tussilago farfara* L., maximum biomass of the plants represented only from 55–60% of their total net dry matter production.

Biomass Production with Time

Plants of the three species started the year's growth with a very similar initial weight (Figs. 1–3) and showed different peaks of maximum dry matter production. Plants collected in Site II (with light grazing) appeared in general to be more productive than those in the more intensely grazed zones (Site I). This was particularly true for *R. repens* which in the lightly grazed zone showed a remarkable exponential growth between April and the middle of June, reaching a peak at the end of this month and then decreasing sharply towards July.

Plants of *R. bulbosus* in the intensely grazed sites showed two clear peaks of

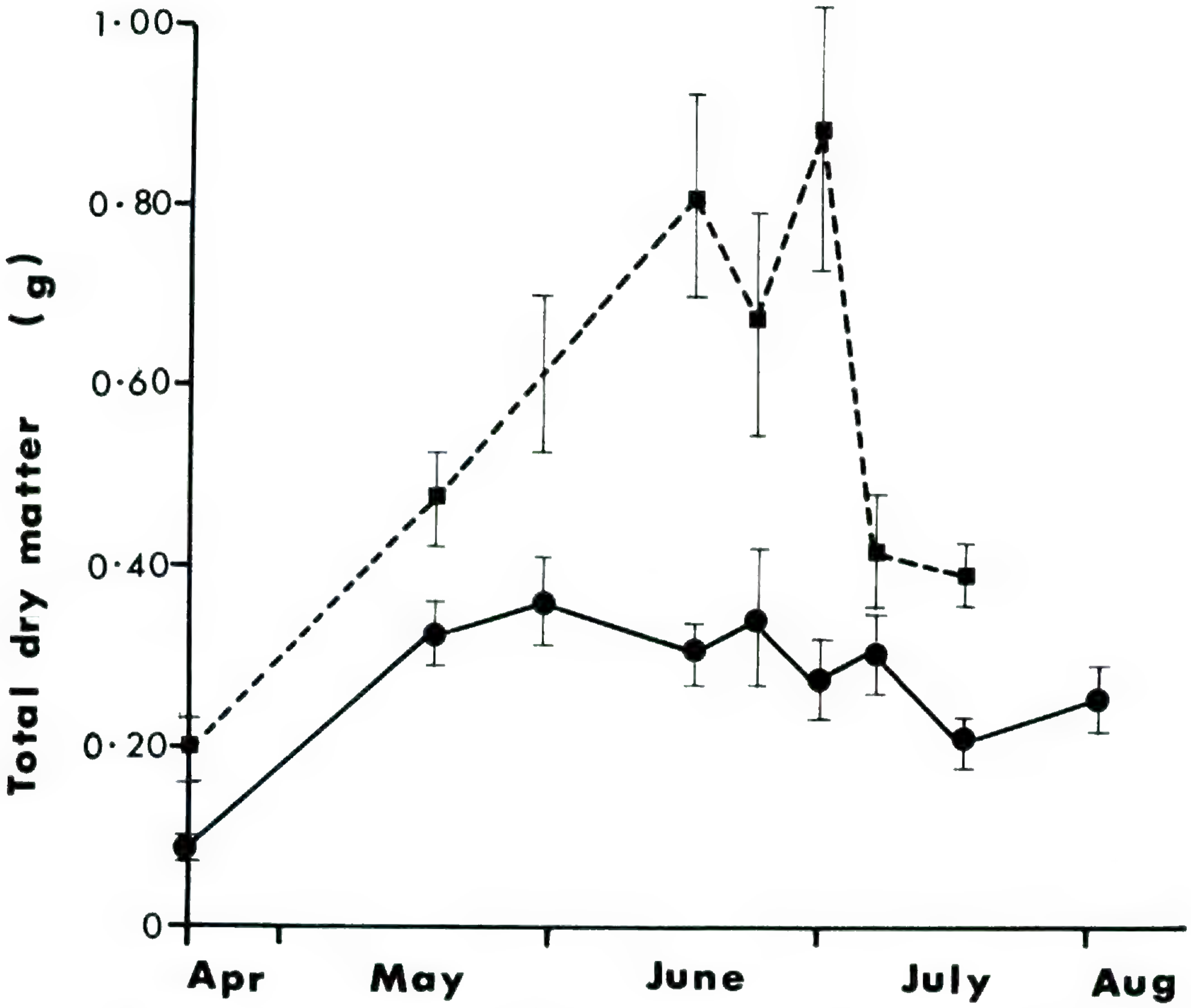

FIGURE 1. Total dry matter produced by plants of *Ranunculus repens* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants, collected in an intensely grazed site (solid squares) and a lightly grazed site (solid circles).

biomass production; the peak occurred earlier in the lightly grazed than in the more intensely grazed sites.

Plants of *R. acris* in the intensely grazed sites also showed two peaks of biomass production in early July and early August and attained the highest weights recorded for any of the three species.

In order to obtain an idea of the "crop" growth rates presented by the three species, the log. of the total dry weight has been plotted in Fig. 4 for the average values of all plants of each species collected in both sites.

Three phases can be distinguished in the curves. The first from April to the end of May or mid-June represents the rapid growth of the winter rosettes at the time of production of new leaves and roots. The second phase, when the growth rate is nearly zero, coincides in *R. repens* with the initiation of stolon growth and elongation and in *R. bulbosus* and *R. acris* with the production of the floral stem carrying floral buds. At this stage, a number of old leaves may have decayed and were probably not collected and may account partly for the reduction in total biomass; the third phase, a negative growth rate, is clearer in *R. repens* and *R. bulbosus*. Many plants of *R. repens* that produce stolons lose all

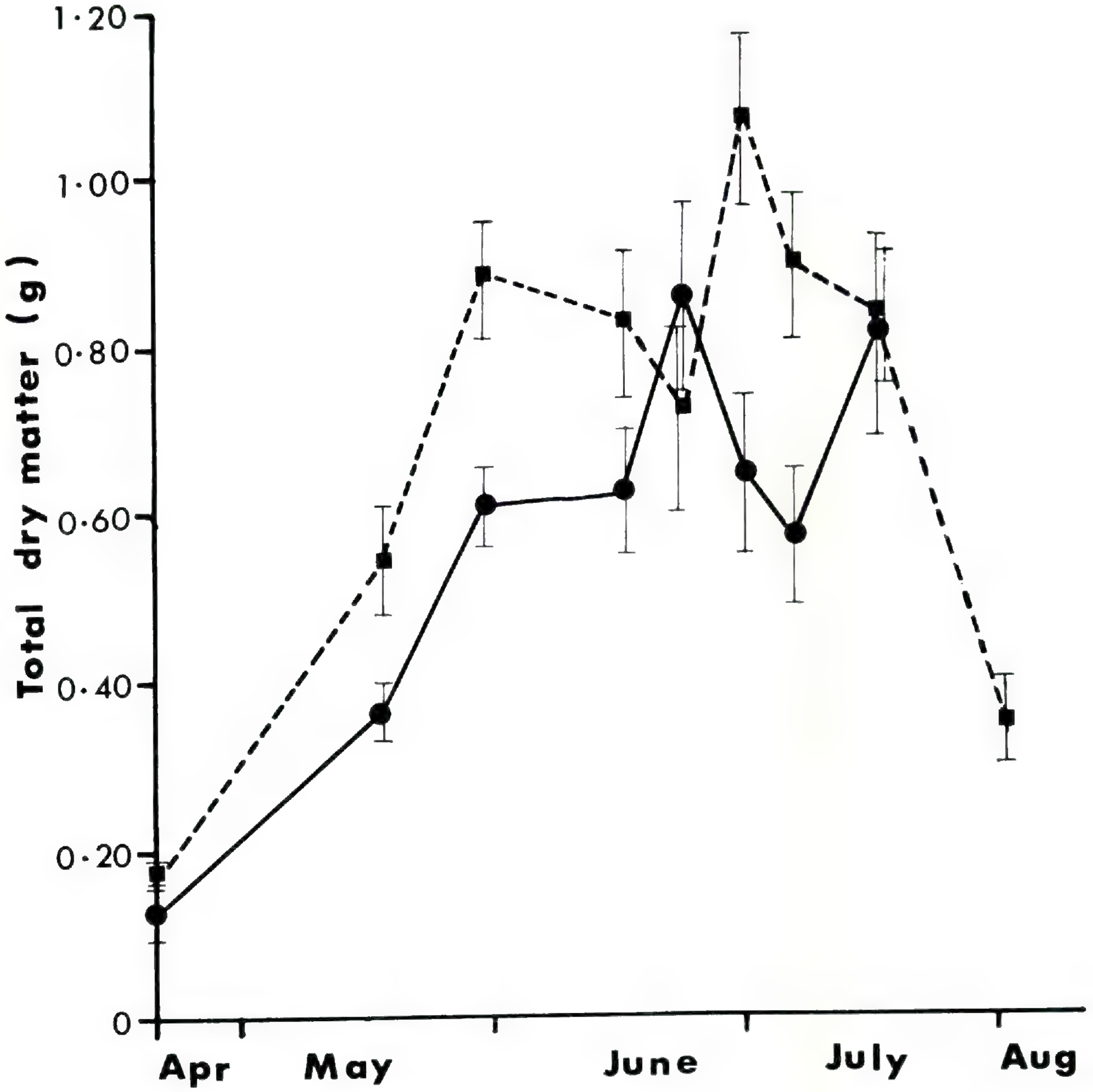

FIGURE 2. Total dry matter produced by plants of *Ranunculus bulbosus* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants, collected in an intensely grazed site (solid squares) and a lightly grazed site (solid circles).

their leaves at this period and eventually die. All the aerial structures of *R. bulbosus* have withered and disappeared by the end of July, when the biomass of these plants is totally represented by the buried corm. This third phase of negative growth rate was not observed for plants of *R. acris* in the study period.

Figures 5–7 show the growth of the different parts of the plants with time. In all the species, the initial period of growth is contributed chiefly by leaves and roots as the plants change from the winter form to the spring form of the rosette. Subsequent growth in *R. repens* is mainly contributed by the production of stolons with their leaves and an increase in the root system that supports the early phases of stolon production. In *R. bulbosus* the corm and the floral stems represented a great proportion of the total dry matter produced by plants from the end of May onwards. There was consistently only a very small growth of the root system.

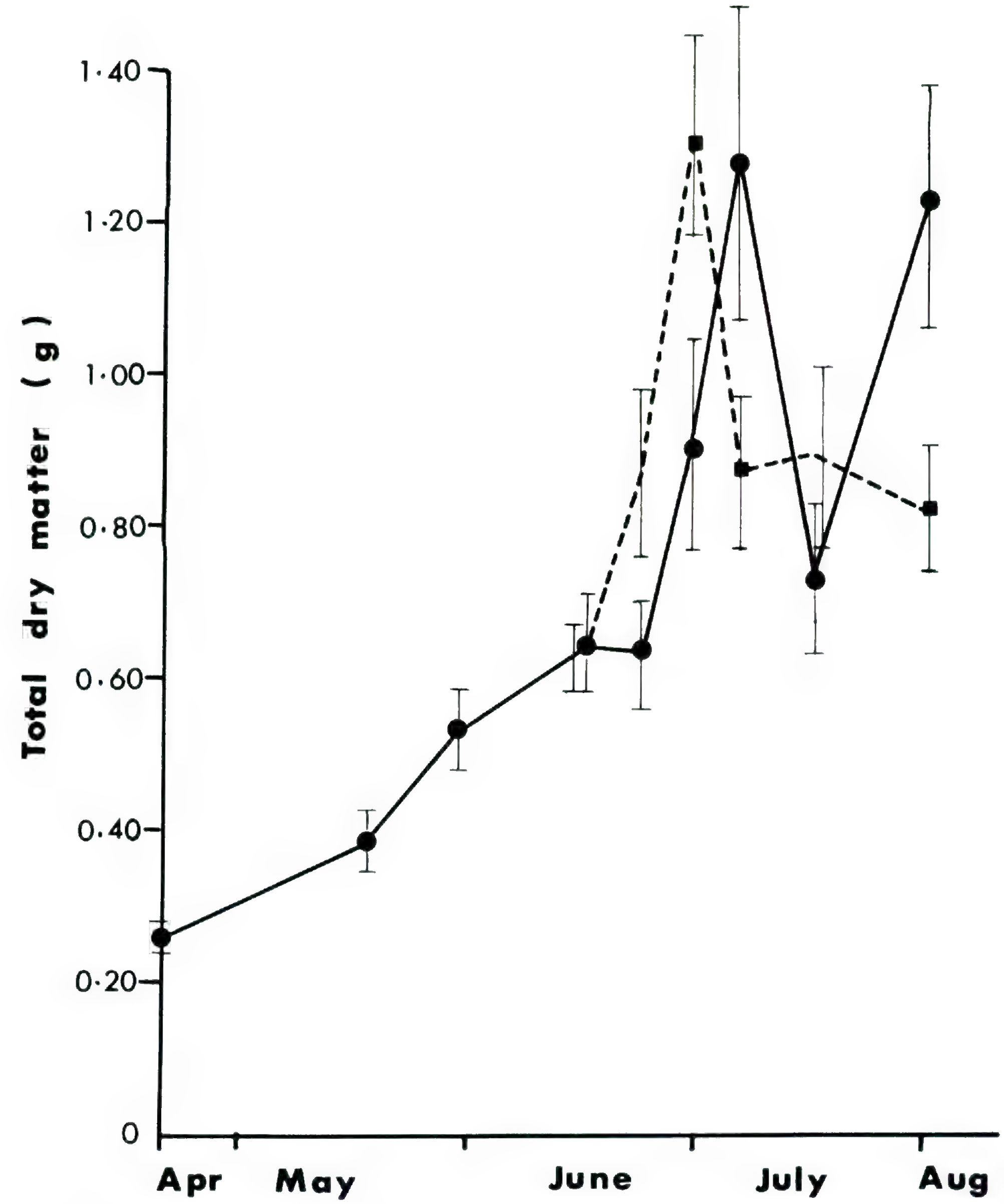

FIGURE 3. Total dry matter produced by plants of *Ranunculus acris* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants, collected in an intensely grazed site (solid squares) and a lightly grazed site (solid circles).

The root system in *R. acris* appeared to be better developed than in the other two species; it contributed a substantial amount of the total biomass. The relative contribution of leaves to the total biomass declined at the end of May when the floral stems together with flowers and achenes become the predominant parts of the total biomass. The similarity between the total weight of flowers plus achenes in plants of *R. bulbosus* and *R. acris* is very striking.

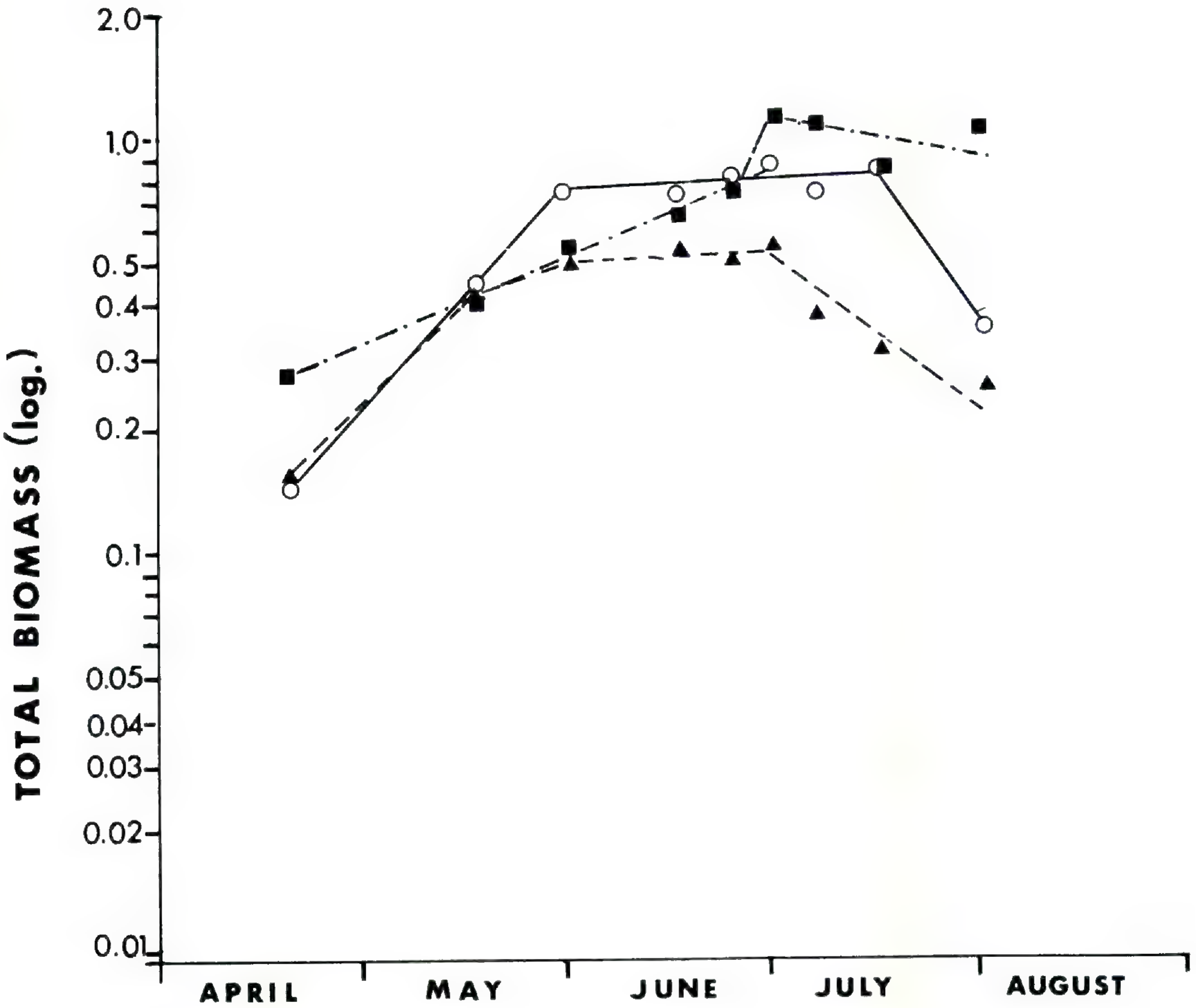

FIGURE 4. Growth rates of plants of *Ranunculus repens* (solid triangles), *R. bulbosus* (open circles), and *R. acris* (solid squares).

THE DISTRIBUTION OF BIOMASS

The patterns of distribution of biomass in plants of the three species of *Ranunculus* are shown in Figs. 8–10. The percentages are derived from averages of 40 plants collected for each species at each date. One of the two more striking points is the difference in dry matter allocated to flowers and seed in *R. repens* —the vegetative reproducer—and *R. bulbosus* and *R. acris*—the seed reproducers. The second point is the similarity of the dry matter allocated to the whole reproductive system of *R. repens* (stolons, stolon leaves, flowers and seed) to the total dry matter allocated to reproduction-related structures in *R. bulbosus* and *R. acris* (floral stems plus flowers and seeds). The constantly low contribution of roots to the total biomass of *R. bulbosus* contrasts with the contribution of roots in the other two species. The high proportion of corm and low proportion of roots in *R. bulbosus* suggest that the summer dormancy of this species may permit it to avoid water stress. It may also be that the roots of *R. repens* and *R. acris* play some of the food storage role that the corm plays in *R. bulbosus*.

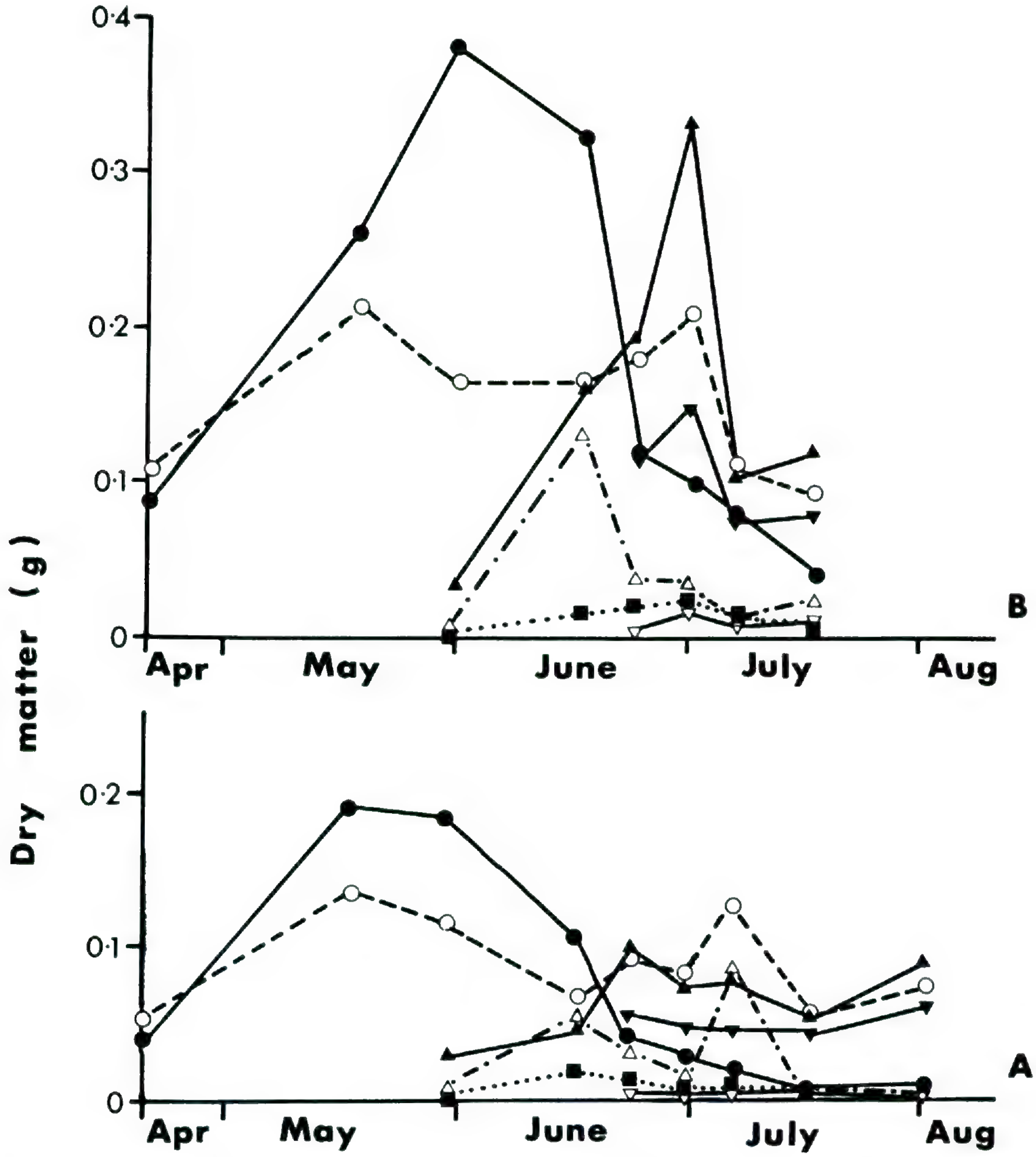

FIGURE 5. Total dry matter produced by the different organs of plants of *Ranunculus repens* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants collected in an intensely grazed site (A) and a lightly grazed site (B). Leaves (solid circles), roots (open circles), stolon leaves (solid triangles pointing downward), stolons (solid triangles, pointing upward), stems (open triangles, dotted lines), flowers (solid squares), and achenes (open triangles, solid lines).

REPRODUCTIVE EFFORT

The proportions of dry matter allocated by each of the three species to: (a) the production of achenes, (b) the production of ancillary structures to sexual reproduction (floral parts, floral stems), and (c) to vegetative propagules (stolons, stolon leaves) are shown in Table 1. It is difficult to assign the stolon leaves definitely as a cost to the parent plant; they may initially be "placental" demand-

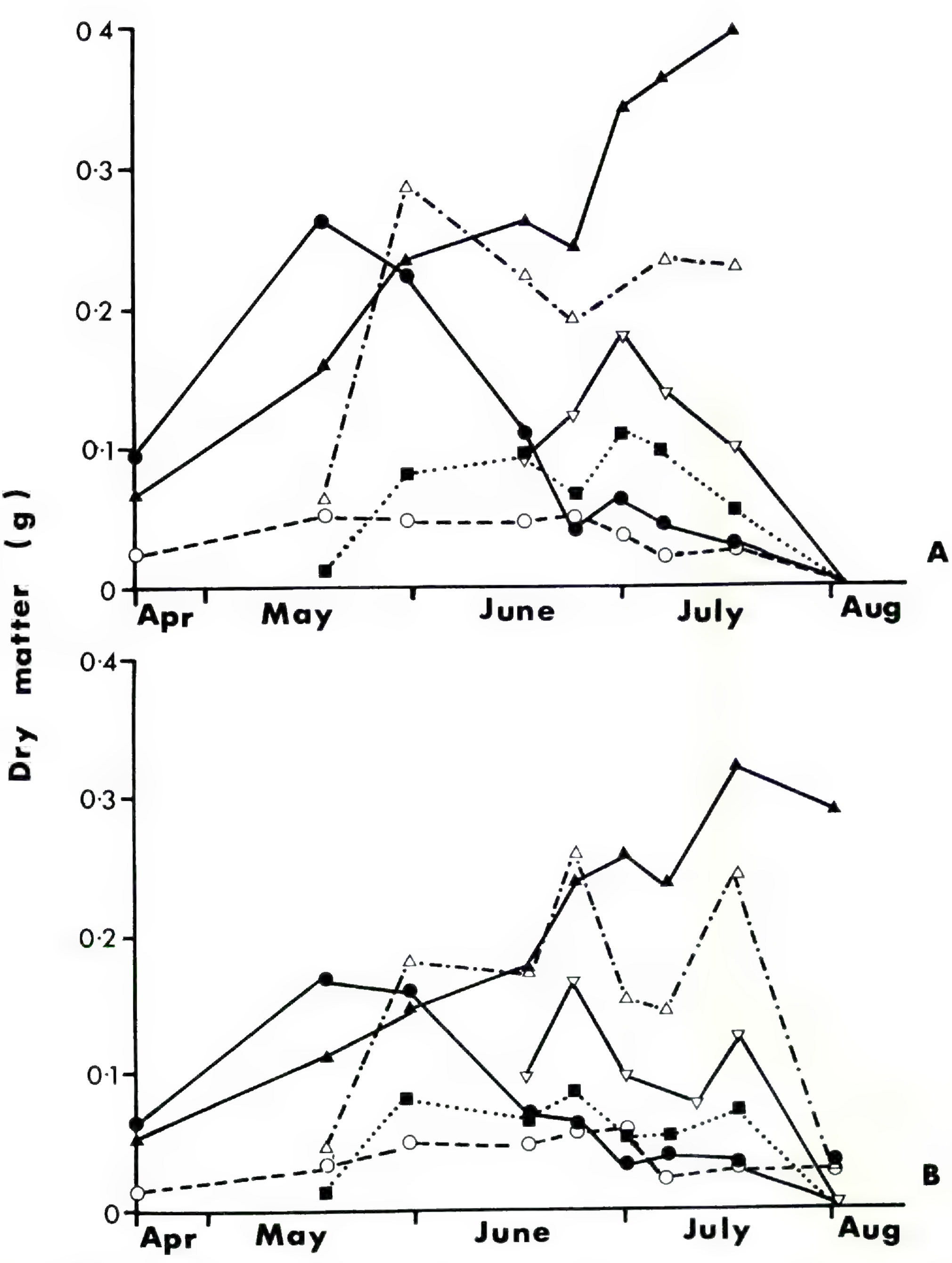

FIGURE 6. Total dry matter produced by the different organs of plants of *Ranunculus bulbosus* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants collected in an intensely grazed site (A) and a lightly grazed site (B). Leaves (solid circles), roots (open circles), corm (solid triangles), stems (open triangles, dotted lines), flowers (solid squares), and achenes (open triangles, solid lines).

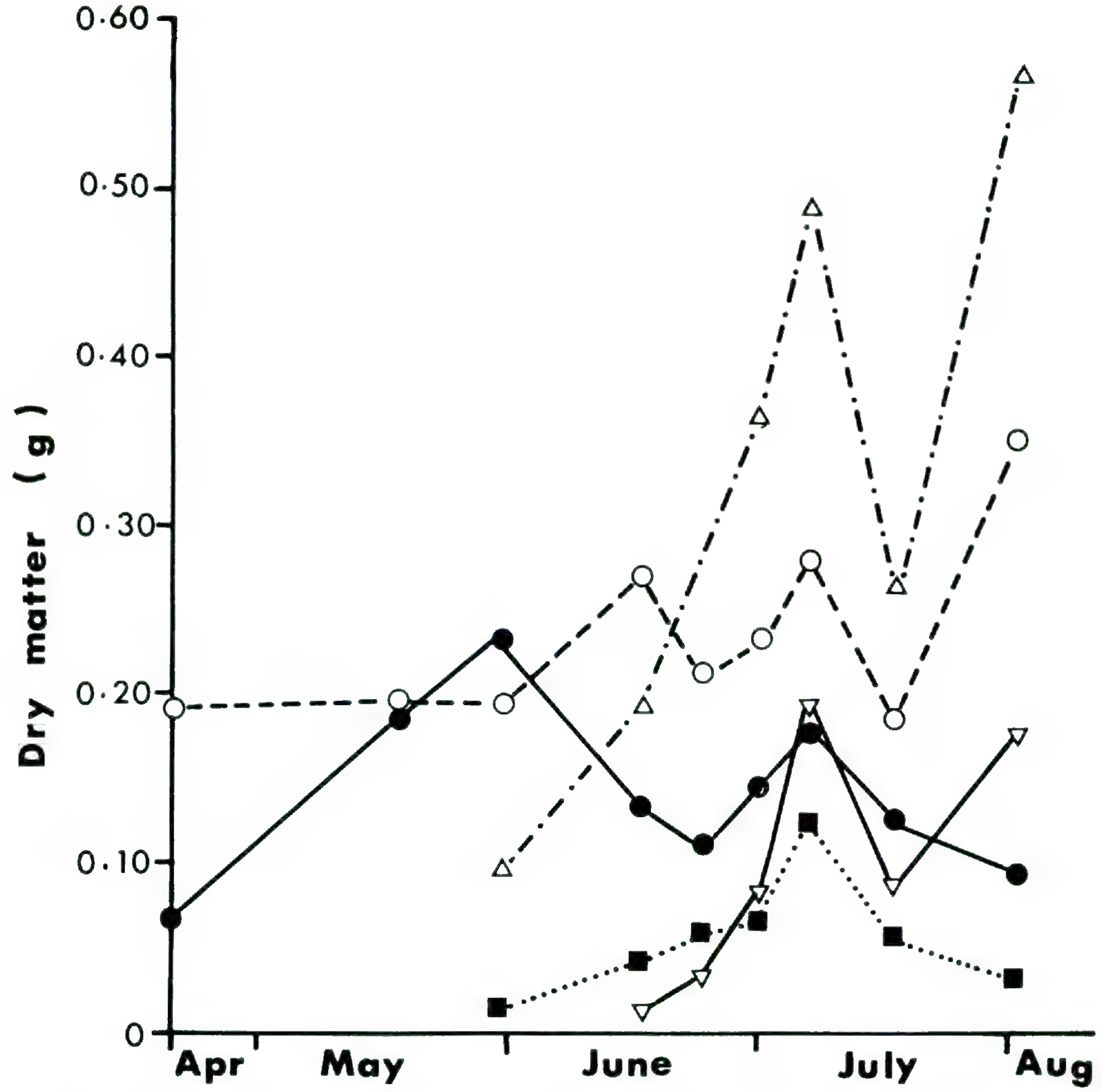

FIGURE 7. Total dry matter produced by the different organs of plants of *Ranunculus acris* between April 20 and August 1, 1969 in a lowland grassland. Each point is the average of 20 plants collected in a lightly grazed site. Leaves (solid circles), roots (open circles), stems (open triangles, dotted line), flowers (solid squares), and achenes (open triangles, solid lines).

ing structures but obviously at some stage acquire a positive assimilatory role. If the proportion of dry matter allocated to achenes only (weight of achenes/total dry weight) as a crude reproductive effort is considered, *R. bulbosus* and *R. acris* appear to have high reproductive efficiency (ca. 15 and 11%, respectively) and *R. repens* has a low reproductive efficiency (between 1 and 5%). However, if dry matter allocated to all propagules (both seed and vegetative) is considered, the situation is different. The three species appear to have "spent" almost the same proportion of their biomass to reproductive ends (either sexual or vegetative); the sum of the allocation to achenes plus ancillary structures plus vegetative reproduction in *R. repens* between June 23 and July 16 varied from 48–58%; the comparable figure in *R. bulbosus* in the same period was 49–52%, and for

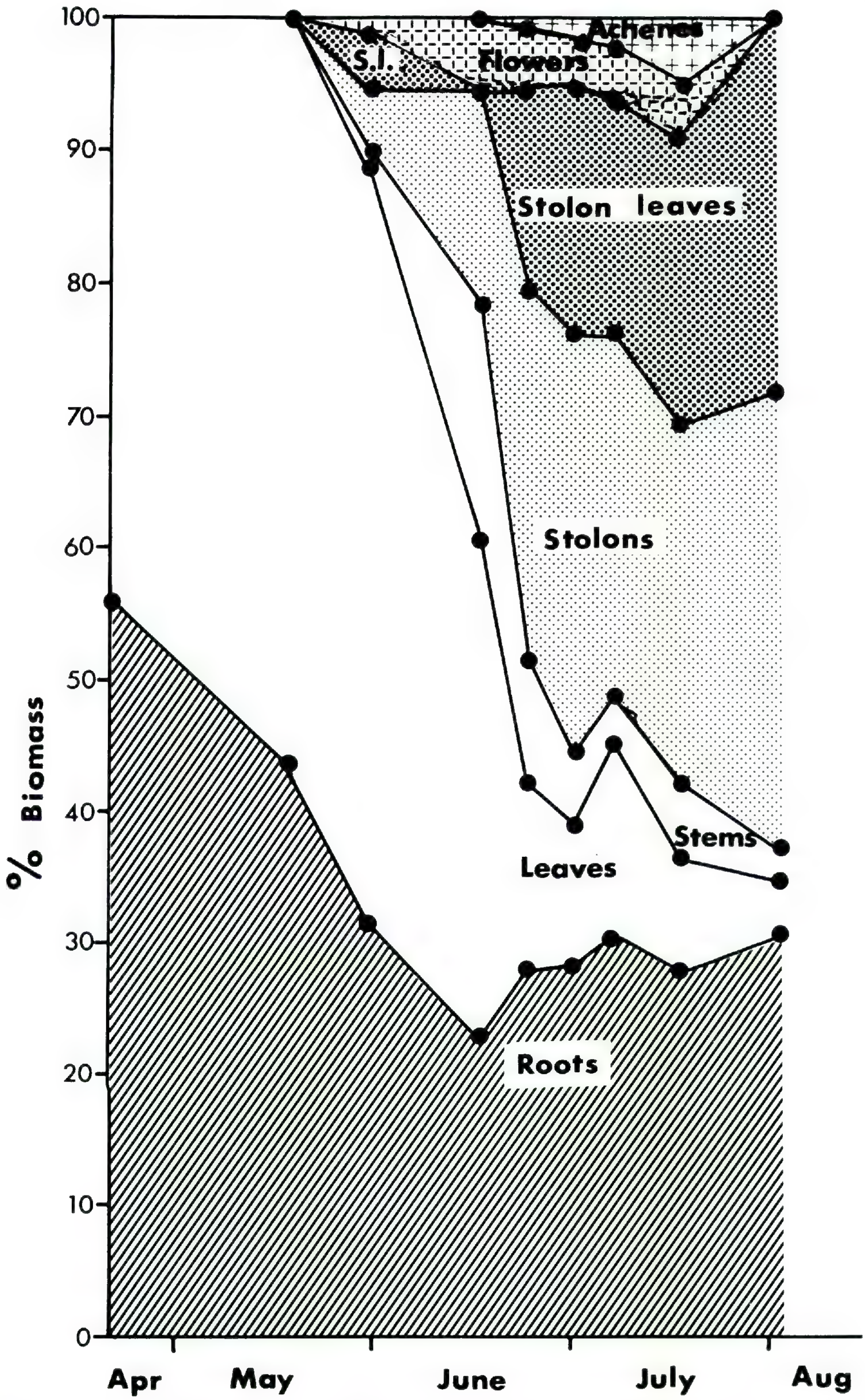

FIGURE 8. Distribution of the total biomass of plants of *Ranunculus repens* to their different organs. Data are averages of 40 plants.

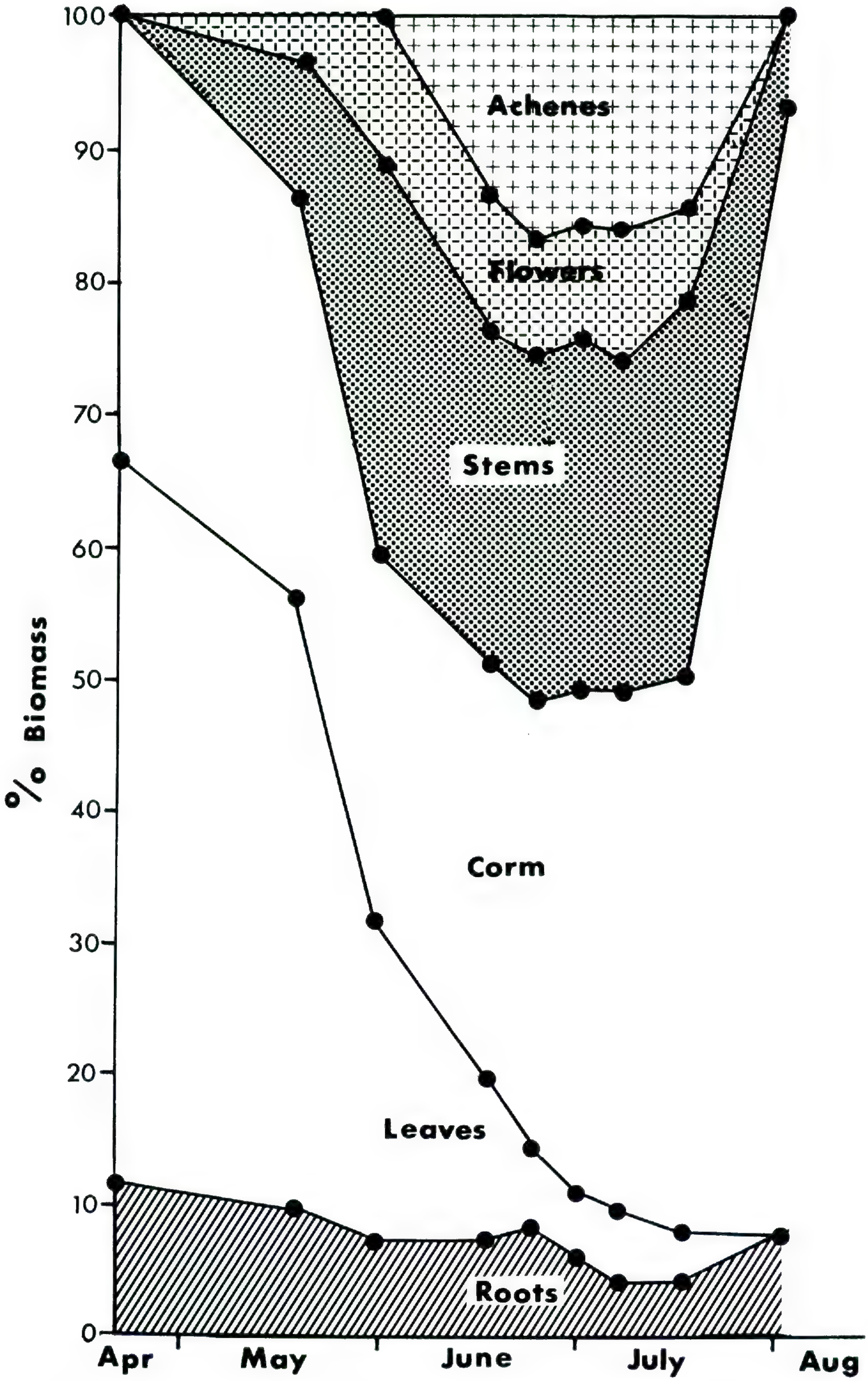

FIGURE 9. Distribution of the total biomass produced by plants of *Ranunculus bulbosus* to their different organs. Data are averages of 40 plants.

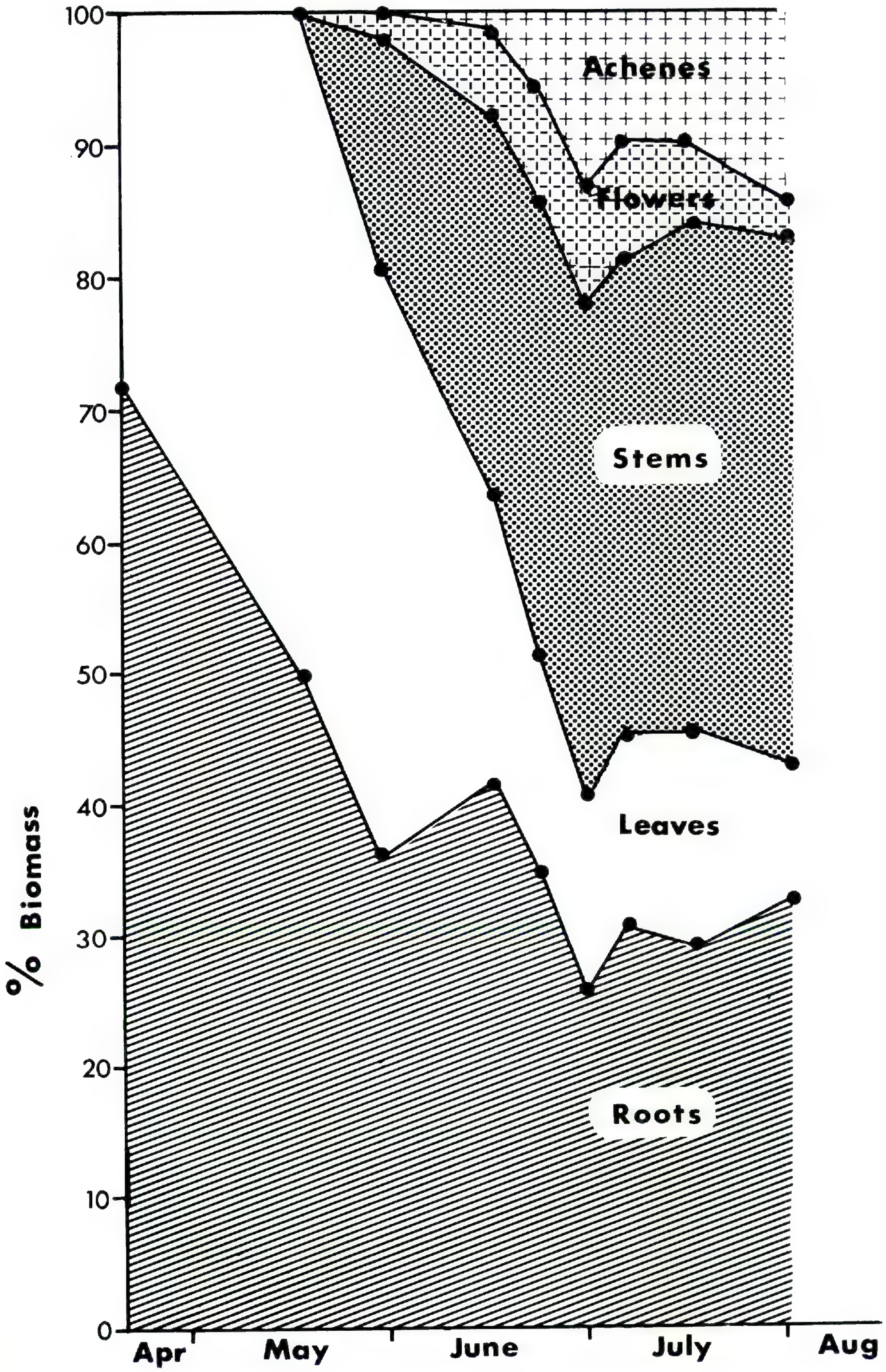

FIGURE 10. Distribution of the total biomass produced by plants of *Ranunculus acris* to their different organs. Data are averages of 20 plants.

TABLE 1. Crude reproductive effort (weight of achenes/total biomass × 100) and % of total biomass allocated to flowers and floral stems and to vegetative reproduction by plants of *Ranunculus repens*, *R. bulbosus*, and *R. acris*. Values for each species are averages of 40 plants.

Date	Achenes only (crude rep. effort)	Flowers and floral stems	Vegetative reproduction	Total reproduction
		R. repens		
29/5	0	2.0	9.4	11.4
16/6	0	4.6	16.9	21.5
23/6	0.8	4.7	43.0	48.5
30/6	1.6	3.4	50.3	55.3
6/7	2.1	4.0	45.1	51.2
16/7	4.8	4.3	48.9	58.0
1/8	0	0	62.9	62.9
		R. bulbosus		
17/5	0	13.8	—	13.8
29/5	0	41.6	—	41.6
16/6	13.3	35.4	—	48.7
23/6	16.8	34.9	—	51.7
30/6	15.7	34.0	—	49.7
6/7	15.9	34.9	—	50.8
16/7	14.0	34.9	—	48.9
1/8	0	0	—	0
		R. acris		
29/5	0	19.2	—	19.2
16/6	1.5	34.7	—	36.2
23/6	5.7	42.7	—	48.4
30/6	13.7	46.2	—	59.9
6/7	9.7	44.8	—	54.5
16/7	9.7	44.3	—	54.0
1/8	14.2	42.7	—	56.9

R. acris it was from 48–60%. It might then be argued that vegetative reproduction in *R. repens* is obtained at the expense of reproduction by seed.

The data on total reproductive effort of the three buttercups, but particularly that of *R. repens*, are in close agreement with information recently obtained for *Hieracium floribundum*, Wimm. & Grab., a perennial, rosette-forming, vegetatively-reproducing species. Thomas & Dale (1974) report for this species in old pastures in Canada a total reproductive effort (inflorescences and stolons) of between 64 and 74% (depending on density stresses) of the dry matter of the plant, excluding the root system, which causes an overestimation of the reproductive effort.

The crude reproductive efficiences obtained for *R. bulbosus* and *R. acris* (Table 1) are very close to those obtained by Struik (1965) for perennial species for woodland and sand barrens in Wisconsin (12 and 15%, respectively), but are considerably lower than the values summarized by Ogden (1968) for weedy cultivated annuals (20–40%). The dry matter produced by reproductive plants of *R. acris* in upland meadows in the Moscow region (Rabotnov & Saurina, 1971) was considerably less (0.5 g) than the plants measured in the present study at College Farm, Aber (0.6–1.3 g).

The following conclusions on dry matter allocation in the three buttercups can be drawn: (a) the rate of growth of *R. repens* and *R. bulbosus* was greater but their growing cycle was shorter than that of *R. acris*; plants of *R. bulbosus* showed the most precocious spring growth; (b) the peaks of growth in the three species occur at different times in coincidence with differences of times at which maximum selection pressures occur; (c) grazing reduced the biomass of *R. repens* but had little effect on the other species; this probably reflects the different palatabilities of the three species; (d) an estimate of reproductive effort must include all the energy allocated by plants to reproduction, whether vegetative or by seed. The vegetative reproducer (*R. repens*) appeared in this respect to have about the same reproductive effort as the seed reproducers (*R. bulbosus* and *R. acris*). Even these two species fall very short of the reproductive efficiency of annuals (Ogden, 1968) and are of the same order as Ogden's values for *Tussilago farfara*. Perhaps the very possession and maintenance of a perennial system involves budgetary costs that are offset by a lower reproductive effort.

Literature Cited

Cody, M. L. 1966. A general theory of clutch size. Evolution 20: 174–184.

Deevey, E. S. 1947. Life tables for natural populations of animals. Quart. Rev. Biol. 22: 283–314.

Donald, C. M. 1962. In search of yield. J. Austral. Inst. Agric. Sci. 28: 171–178.

Gadgil, M. & Solbrig, O. T. 1972. The concept of "r" and "K" selection: evidence from wild flowers and some theoretical considerations. Amer. Naturalist 106: 14–31.

Harper, J. L. 1957. Biological flora of the British Isles. *Ranunculus acris* L., *Ranunculus repens* L. and *Ranunculus bulbosus* L. J. Ecol. 45: 289–342.

———. 1967. A Darwinian approach to plant ecology. J. Ecol. 55: 247–270.

——— & D. Gajic. 1961. Experimental studies on the mortality and plasticity of a weed. Weed Res. 1: 91–104.

——— & J. Ogden. 1970. The reproductive strategy of higher plants. I. The concept of strategy with special reference to *Senecio vulgaris* L. J. Ecol. 58: 681–698.

——— & J. White. 1971. The dynamics of plant populations. Pp. 41–61, *in* Dynamics of Populations. Proceedings of the Advanced Study Institute on "Dynamics of Numbers in Populations." Oosterbeck, Wageningen.

——— & ———. 1974. The demography of plants. Annual Rev. Ecol. Syst. 5: 419–463.

Hartshorn, G. S. 1972. The ecological life history and population dynamics of *Pentaclethra macroloba*, a tropical wet forest dominant, and *Stryphnodendron excelsum* an occasional associate. Ph.D. thesis, Univ. of Washington, Seattle, Washington.

Hawthorn, W. R. 1973. Population dynamics of two weedy perennials, *Plantago major* L. and *P. rugelli* Decne. Ph.D. thesis, Univ. of West Ontario, London, Ontario.

Hett, J. M. & O. L. Loucks. 1971. Sugar maple (*Acer saccharum* Marsh.) seedling mortality. J. Ecol. 59: 507–520.

Kays, S. & J. L. Harper. 1974. The regulation of plant and tiller density in a grass sward. J. Ecol. 62: 97–105.

Langer, R. H. M. 1956. Growth and nutrition of timothy (*Phleum pratense*). The life history of individual tillers. Ann. Appl. Biol. 44: 166–187.

MacArthur, R. H. & E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton Univ. Press, Princeton, New Jersey.

Ogden, J. 1968. Studies on reproductive strategy with particular reference to selected composites. Ph.D. thesis, University of Wales.

———. 1970. Plant population structure and productivity. Proc. New Zealand Ecol. Soc. 17: 1–19.

Rabotnov, T. A. 1950. Life cycles of perennial herbage plants in meadow communities. Proc. Komarov Bot. Inst. Acad. Sci. USSR, ser. 3, 6: 7–240.

———. 1956. The life cycle of the *Heracleum sybiricum* L. Bjull. Moskovsk Obšš. Isp. Prir., Otd. Biol. 61: 73–80.

——— & N. I. SAURINA. 1971. The density and age composition of certain populations of *Ranunculus acris* L. and *R. auricomus* L. Bot. Zurn. (Moscow & Leningrad) 56: 476–484.

SAGAR, G. R. 1959. The biology of some sympatric species of grassland. D. Phil. thesis, University of Oxford, Oxford.

——— & A. M. MORTIMER. In press. The population dynamics of plants.

SARUKHÁN, J. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. II. Reproductive strategies and seed population dynamics. J. Ecol. 62: 675–716.

——— & M. GADGIL. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. J. Ecol. 62: 921–936.

——— & J. L. HARPER. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L., and *R. acris* L. I. Population flux and survivorship. J. Ecol. 61: 675–716.

SHARITZ, R. R. 1970. Population dynamics of two competing plant species. Ph.D. thesis, Univ. of North Carolina, Chapel Hill, North Carolina.

STERN, W. R. & D. F. BEECH. 1965. The growth of safflower (*Carthamus tinctorius* L.) in a low altitude environment. Austral. J. Agric. Res. 16: 801–816.

STRUIK, G. J. 1965. Growth patterns of some native annual and perennial herbs in Southern Wisconsin. Ecology 46: 401–420.

SYMONIDES, E. 1974. Populations of *Spergula vernalis* Willd. on dunes in the Torun basin. Ekol. Polska 22: 379–416.

TAMM, C. O. 1956. Further observations on the flowering and survival of some perennial herbs. Oikos 7: 273–292.

THOMAS, A. G. & H. M. DALE. 1974. Zonation and regulation of old pasture populations of *Hieracium floribundum*. Canad. J. Bot. 52: 1451–1458.

WERNER, P. A. 1975. Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). Oecologia 20: 197–201.

WHITE, J. 1975. Patterns of thinning of plant populations. Twelfth International Botanical Congress, Leningrad, July 1975, ms. 5 + vi pp.

——— & J. L. HARPER. 1970. Correlated changes in plant size and number in plant populations. J. Ecol. 58: 467–485.

YODA, K., T. KIRA, H. OGAWA & K. HOZUMI. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka City Univ. 14: 107–129.

BARNARDIELLA: A NEW GENUS OF THE IRIDACEAE AND ITS RELATIONSHIP TO *GYNANDRIRIS* AND *MORAEA*[1]

PETER GOLDBLATT[2]

ABSTRACT

The discovery of the presence of a sterile ovary tube in a plant known both as *Homeria herrei* and *Gynandriris spiralis* led to a detailed study of the characteristics of this species. A chromosome number of $n = 10$ suggests that the species belongs neither to *Homeria* or *Gynandriris* but may have been derived from the genus *Moraea* independently, though it has characteristics of *Homeria* and *Gynandriris*. The species is thus assigned to a new genus as *Barnardiella spiralis* (N.E. Br.) Goldblatt.

In the course of field studies on South African Iridaceae, I was surprised to discover that the fairly common Namaqualand species known as *Homeria herrei* possessed a well-developed ovary tube, a fact not noted in the description of this plant (Bolus, 1931). Careful examination of living plants and subsequently of ample herbarium material showed this character in all specimens, and confirmed that this unusual feature is exactly like the sterile prolongation of the ovary which characterizes and partly defines the genus *Gynandriris*.

A cursory review of all the species of *Gynandriris* revealed that the long overlooked *G. spiralis* (N.E. Br.) Foster described by Baker in 1892 as a *Moraea*, in which genus it is an illegitimate homonym, matched *Homeria herrei* exactly. With the combination in *Gynandriris* already made, *H. herrei* could simply have been reduced to synonymy. However, living material on hand enabled further examination and this confirmed Bolus's description of the flower as being like that in the genus *Homeria*, i.e., lacking clear distinction between the inner and outer tepals, and without the typical petaloid style branches and paired crests (Fig. 1 B) of both *Gynandriris* and *Moraea*, the probable ancestor of *Gynandriris*.

The presence in this one species of the distinguishing characteristics of two genera immediately posed the problem of the true relationship of *Gynandriris spiralis*/*Homeria herrei*. The genus probably ancestral to both *Homeria* and *Gynandriris* is *Moraea* (Goldblatt, 1971). *Homeria* is believed to have evolved from *Moraea* by reduction of the broad petaloid style branches and long, paired style crests and by a change from distinct inner and outer tepal whorls to ± equal tepals (Fig. 1A) (Goldblatt, 1971). In contrast, *Gynandriris* has a flower exactly like many species of *Moraea* except that the ovary is extended upwards to form a sterile tube, and with the development of the ovary tube the pedicels are much reduced in length (Fig. 1 B).

The question with regard to *Homeria herrei* is whether it is more closely re-

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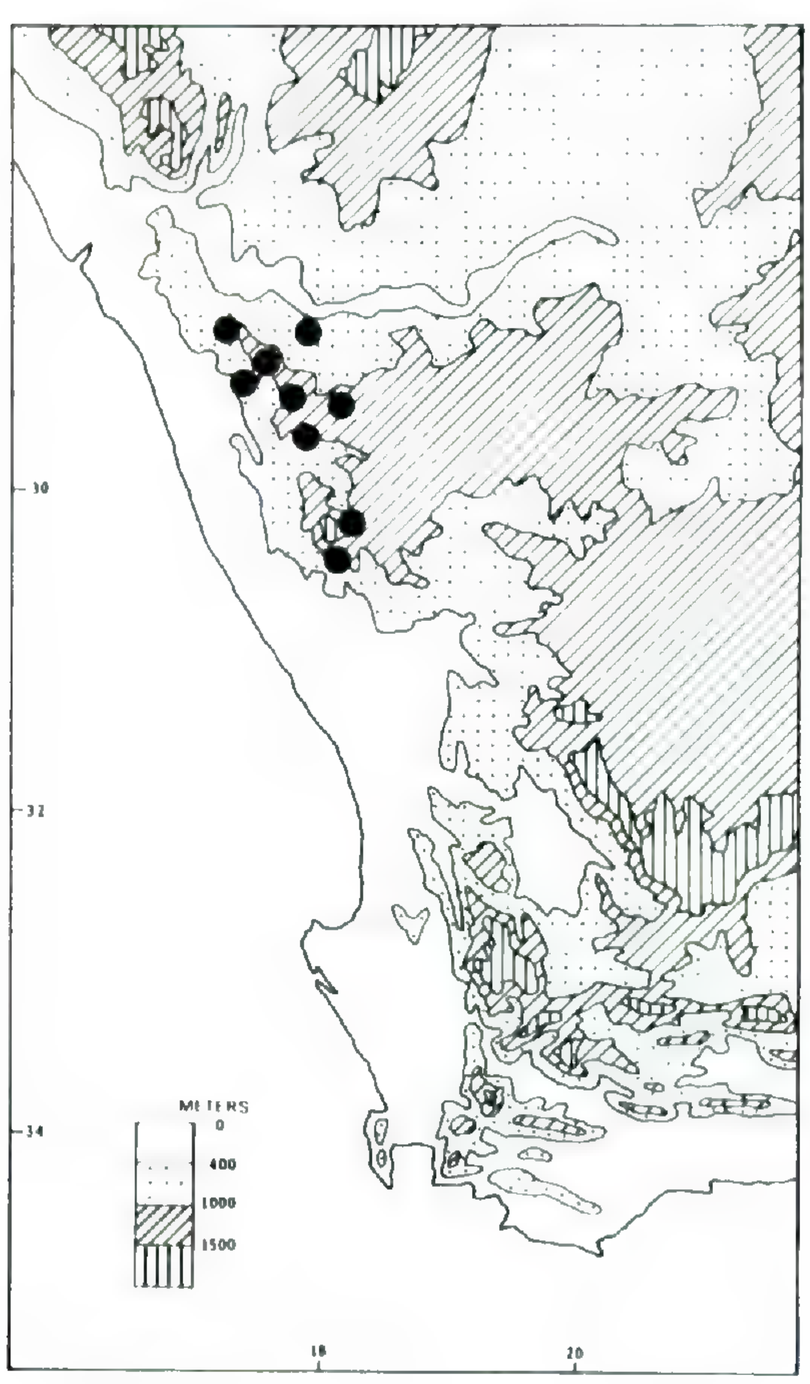

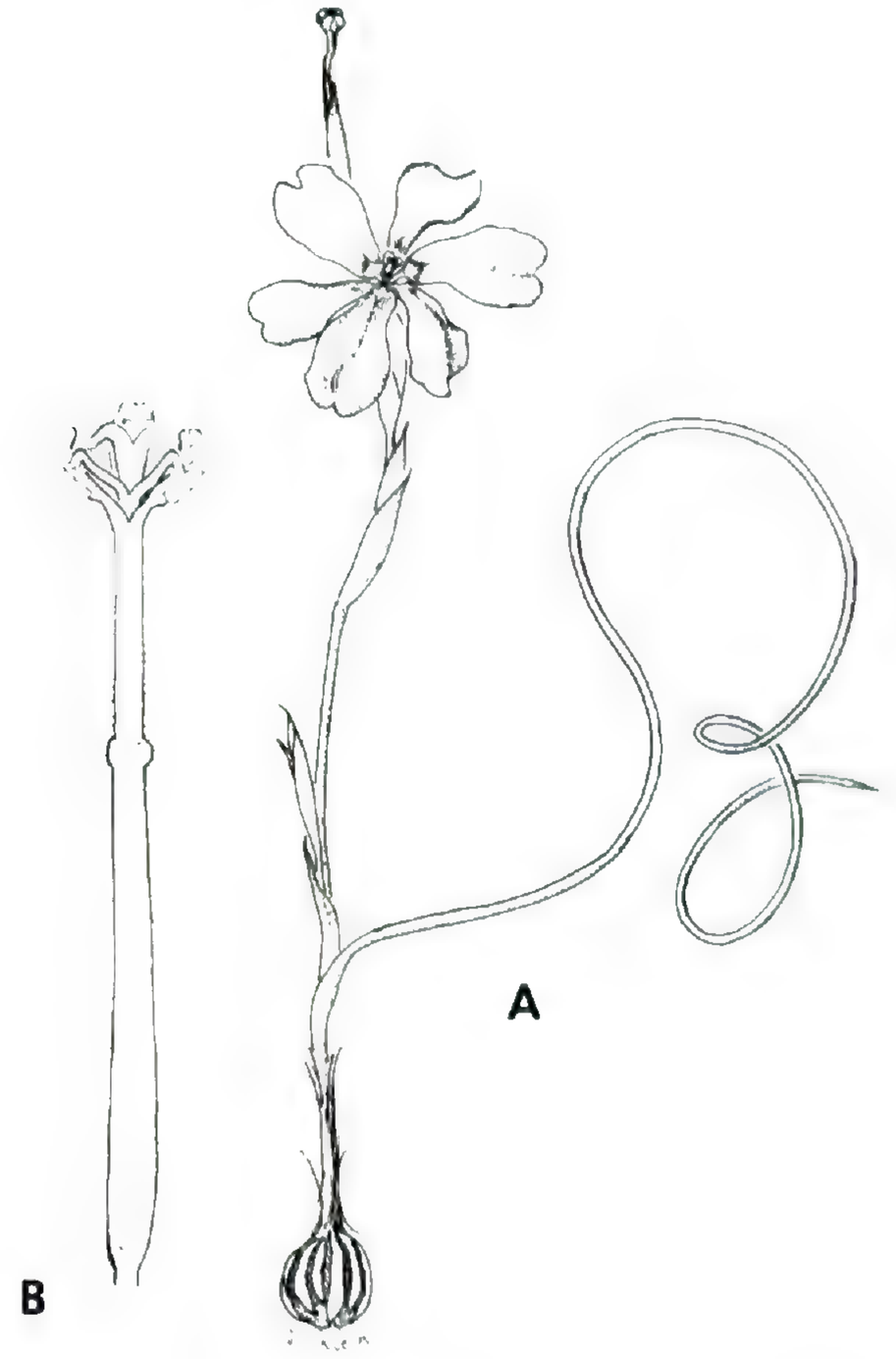

FIGURE 1. Morphology and distribution of *Barnardiella spiralis*.—A. Whole plant ($\times \frac{2}{3}$). —B. Androecium and gynoecium ($\times 7$).

lated to *Homeria*, in fact a *Homeria* with an ovary tube, or a derivative of *Gynandriris*, having a simplified flower. The first possibility assumes independent origin of the ovary tube in *Gynandriris* and in a single species of *Homeria*, while the second presupposes the reduction of the style branches and crests independently in the ancestors of *Homeria* and in one specialized species of *Gynandriris*. The latter seems more likely since species of *Moraea* with partly to entirely reduced style branches and crests are known and these are certainly derived independently of *Homeria*.

An answer to this question was sought by a chromosome study which seemed promising as both *Homeria* and *Gynandriris* are quite well known cytologically (Goldblatt, 1971). *Gynandriris*, with a basic chromosome number of $x = 6$, has a characteristic karyotype with one or two metacentric chromosomes and a very large satellite. *Homeria*, also with $x = 6$, has by contrast only submetacentric to acrocentric chromosomes and one or two usually small satellites.

CYTOLOGY

The following two collections were studied, one kindly provided by Kirstenbosch Botanical Gardens, Cape Town, South Africa, and the other collected by myself in South Africa. Mitotic studies on root tips were made following the method described previously (Goldblatt, 1976a).

Barnardiella spiralis (N.E. Br.) Goldblatt, $2n = 20$. SOUTH AFRICA. Cape: Namaqualand, near Steinkopf, *Wisura 3891* (NBG). Namaqualand, south of Nababeep, *Goldblatt 3066* (MO).

The cytological findings were startling: *Gynandriris spiralis*, with $n = 10$, proved to have a karotype unlike either *Homeria* or *Gynandriris*, all species known cytologically having $x = 6$. Consequently it seemed the question relating to the origin of *G. spiralis* could not be explained in either of the two ways already discussed.

A base number of $x = 10$ is however known in the large genus *Moraea* in which the primitive members of the genus, subgenera *Moraea*, *Monocephalae* and *Visciramosa*, all have a base number of $x = 10$, while the more specialized species assigned to subgenera *Vieusseuxia* and *Grandiflora* have $x = 6$ (Goldblatt, 1976a). It seems reasonable that the so called *G. spiralis* could have been derived directly from one of the primitive subgenera of *Moraea*, especially as its karyotype, with five acrocentric long and five very short pairs of chromosomes, is not unlike that in *M. serpentina* Baker and *M. tortilis* Goldblatt ined. of sect. *Moraea* and in several species assigned to sect. *Deserticola* (Goldblatt, 1976b), where four (or occasionally five) long acrocentric and six (or five) much shorter chromosome pairs occur. Accepting this hypothesis for the origin of *G. spiralis*, it seems that both the sterile ovary beak and the reduced flower, especially the style, evolved independently in this species and in *Gynandriris* and *Homeria*, respectively. If so, consistent generic treatment compels the recognition of *G. spiralis* as a distinct genus.

MORPHOLOGY

Morphological comparison between *Gynandriris*, *Moraea*, and *Homeria* gives no reason to doubt the contention that *G. spiralis* should be placed in a distinct genus. Features shared with *Gynandriris* proper extend no further than the beaked ovary tube. The single, terete leaf, flower with subequal tepals and crestless style branches, and especially the brown, firm inflorescence spathes are all unknown in *Gynandriris*, which has particularly distinctive spathes that are membranous, transparent and conspicuously veined. The latter difference in particular provides strong grounds for distinguishing *G. spiralis* from the rest of *Gynandriris*.

Homeria, a larger genus, comprises a range of morphological types and a few representatives are as diminutive and small flowered as *G. spiralis*. *Homeria rogersii* L. Bol. in particular approaches it in general form. As is typical in *Homeria*, *H. rogersii* has an ordinary short green ovary, and a single leaf, which in this species is terete; it also has a base number of $x = 6$, like all other species of the genus. Except for the great difference in chromosome number with $x = 6$ in *Homeria* and $x = 10$ in *Gynandriris spiralis*, a species such as *H. rogersii* might easily be envisaged as ancestral to *G. spiralis*.

A comparison with the very large and varied genus *Moraea* confirms that the corm, terete leaf form, and spathes of *Gynandriris spiralis* do conform in a general

way to species such as *M. serpentina*, *M. tortilis*, as well as *M. bolusii* Baker and *M. macgregorii* Goldblatt ined., and their allies (all subgen. *Moraea* with $x = 10$). These species of *Moraea* have dark corm tunics like those in *G. spiralis*, otherwise not common in *Moraea*, and are rather small and few branched, with narrow to terete leaves. Another reason for accepting forms such as these as possible ancestors is that the reduction of the style branches and crests does occur within *Moraea* itself. This is believed to have occurred independently several times, giving rise to *Homeria*-like species, e.g., *M. elsiae*, forms of *M. odorata*, and *M. insolens*, while the genus *Homeria* has been suggested to have evolved from *Moraea* (Goldblatt, 1971) in this way. Thus the reduced style and subequal tepals could equally have had an independent origin from *Moraea*, as from *Homeria*.

Morphological evidence then seems equally strong in supporting the origin of *Gynandriris* from *Homeria* or *Moraea*, but weaker in the case of *Gynandriris*. Taken together with the chromosomal data, it is however difficult not to accept the conclusion that forms such as *M. serpentina* or *M. tortilis* in subgen. *Moraea* are the most likely ancestors. Regardless of which genus is ancestral, generic recognition is called for and this plant is assigned to the new genus *Barnardiella*, named in honor of Professor T. T. Barnard, a recognized expert on Iridaceae, and long-time student of the nomenclatural history of South African plants. In naming this genus after him, I wish to acknowledge personally his help and guidance in my own studies of the Iridaceae.

TAXONOMY

Barnardiella Goldblatt, gen. nov.

Caudex cormus, nigris tunicis. Folium solitarium, base insertum. Scapus pauciramosus, rami sessiles. Spatha pallida, brunnea, membranacea, costis obscuris. Flos stellatus; tepala subaequales, patentes. Filamenta connata. Ovarium cylindricum, fecundum in base, prolongatum supra tubo sterile. Rami stylis teretes, apices bifurcati, lobi breaves, angusti, divergentes.

Rootstock a corm, with dark tunics. Leaf solitary, inserted at the base. Scape few branched, branches sessile. Spathes dry, pale brown, without prominent veins. Flower stellate; tepals subequal, spreading. Filaments connate. Ovary cylindrical, fertile at base only, prolonged upwards as a sterile beaklike tube. Style branches short, terete, dividing into two diverging, narrow apically stigmatic arms. Chromosome number $2n = 20$.

Type species: *Bernardiella spiralis* (N.E. Br.) Goldblatt

Only one species, distributed in Namaqualand, South Africa.

Barnardiella spiralis (N.E. Br.) Goldblatt, comb. nov.

Helixyra spiralis N.E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929. TYPE: as for *M. spiralis* Baker.

Moraea spiralis Baker, Handbook Irid. 55. 1892, nom. illeg., non *M. spiralis* L.f., 1781. TYPE: South Africa, Cape, Namaqualand, *Drege 2604* (K, lectotype; BOL, isotype). *Morris s.n.* (BOL-5788, paratype).

Gynandiris spiralis (N.E. Br.) Foster, Contr. Gray Herb. 114: 41. 1946.

Homeria herrei L. Bol, S. African Gard. 21: 367. 1931. TYPE: South Africa, Cape, Breekpoort, Steinkopf, Namaqualand, *Herre s.n.* (BOL, holotype).

Distribution: Namaqualand, sandy soils from Bitterfontein in the south to Steinkopf in the north (Fig. 1).

Literature Cited

Baker, J. G. 1892. Handbook of the Irideae. George Bell, London.
Bolus, H. M. L. 1931. Plants new or noteworthy. S. African Gard. 21: 367–368.
Goldblatt, P. 1971. Cytological and morphological studies in the southern African Iridaceae. J. S. African Bot. 37: 317–460.
———. 1976a. Evolution, cytology and subgeneric classification in *Moraea* (Iridaceae). Ann. Missouri Bot. Gard. 63: 1–23.
———. 1976b. The genus *Moraea* in the winter rainfall region of southern Africa. Ann. Missouri Bot. Gard. 64: in press.

CHROMOSOME CYTOLOGY OF *HESSEA*, *STRUMARIA*, AND *CARPOLYZA* (AMARYLLIDACEAE)

PETER GOLDBLATT[1]

ABSTRACT

A diploid number of $2n = 20$ is reported in *Carpolyza*, in the four species of *Strumaria*, and four of the five species of *Hessea* studied. One species, *Hessea zeyheri*, has $2n = 22$. Similarity of karyotypes in all the species with $2n = 20$ appears to indicate a close relationship between them. *Hessea zeyheri* with $2n = 22$ may be a link between the $x = 10$ group and the remainder of the tribe Amaryllideae in which $x = 11$ is basic. The possible systematic significance of the difference in base number in *Hessea zeyheri* is explored and a reevaluation of generic limits is suggested.

The genera of *Hessea*, *Strumaria*, and *Carpolyza* comprise what seems a natural alliance in the Amaryllidaceae. Their overall geographical range is limited to the drier regions of southern Africa, including the winter rainfall region of the Cape Province. The three genera share the following characteristics: a bulb with fibrous tunics of the *Crinum* type; small, white to pink, ± actinomorphic flowers, perianth tube short or lacking; distinctive soft fleshy seeds, such as are found in the tribe Amaryllideae[2], which break through the poorly developed capsule even before they mature. *Hessea* and *Strumaria*, as presently circumscribed, each comprise approximately ten species while *Carpolyza* is monotypic. *Carpolyza* is very distinct, but generic differences between *Hessea* and *Strumaria* are not clear and appear in need of reevaluation.

In spite of the contrary opinions of systematists such as Hutchinson (1959) and the earlier workers, Pax & Hoffmann (1930), and Herbert (1837), I am convinced that *Hessea*, *Strumaria*, and *Carpolyza* are closely related, and that their affinities lie with the tribe Amaryllideae, which includes amongst others, *Amaryllis*, *Crinum*, and *Nerine*. The characters shared are such fundamental features as the peculiar fibrous bulb tunics and fleshy, soft seeds. This relationship has only recently been recognized by Traub (1965), who places all three genera in the Amaryllideae (which he treats as Crineae).

The present cytological study is an attempt to obtain more information on the relationships of the three genera to one another and to the tribe Amaryllideae. Until now the cytology of only two species was known (Wilsenach, 1965) and, as is now clear, neither record is representative of the group as a whole. The

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[2] I am compelled to accept the opinions and conclusions of Sealy (1939), Dyer (1954) and Dandy & Fosberg (1954) regarding the identity of *Amaryllis belladona* L., the type of the Amaryllidaceae, i.e., applied to the S.W. Cape species. In contrast, Uphof (1938), Traub (1954, 1963), and Traub & Moldenke (1949) regard the species as a New World plant (= *Hippeastrum*). The arguments raised by Uphof, Traub, and Moldenke, correct up to a point, ignore the existence of a specimen of the Cape plant in the Cliffort Herbarium which almost certainly is the holotype. A detailed discussion of the opposing arguments need not be repeated, as the evidence has been fully presented elsewhere. In the terminology of Traub, Crineae is equivalent to the Amaryllideae as used here.

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present work comprises chromosomal data on ten species in all three genera, ± half of the species in the alliance. Species are all relatively rare and local, do not bloom regularly, and are thus very difficult to obtain. I hope eventually to collect further species for study but results at the present time merit publication, as there is no reason to believe further species will come to hand in the foreseeable future.

Methods and Materials

Plants used in this study were all collected in the wild. Some had been in cultivation at the Kirstenbosch Botanical Gardens, Cape Town, South Africa, for a short time. Mitotic preparations only were made, root tips being collected from sprouting bulbs or from germinating seeds.

The same cytological technique as described earlier for the genus *Nerine* (Goldblatt, 1972) was employed, involving pretreatment in 0.05% colchicine, maceration in 10% HCl and squashing in lacto-propionic orcein.

Cytology

A basic chromosome number of $x = 10$ for the three genera seems indicated (Table 1) with $2n = 20$ found in all but one of the species studied (Figs. 1–2). The exception, *Hessea zeyheri*, is problematic; three populations were examined and a diploid number of $2n = 22$ seems most likely. While $2n = 22$ was the lowest number found, some plants in all three populations have $2n = 23$, 24, or even 25; $2n = 24$ was reported by Wilsenach (1965) for this species. The reason for proposing $2n = 22$ as the correct diploid number in *H. zeyheri* is not only that this was the lowest number encountered in the species, but where this number was exceeded, the extra chromosomes were quite small and appeared to lack centromeres. This makes it very likely that these are supernumeraries, and they are here regarded as B-chromosomes. Other workers have also encountered B-chromosomes in the Amaryllideae, notably Jones & Smith (1967) who recorded them in *Crinum*. Since $x = 11$ is almost certainly basic in the tribe, reports of $2n = 24$ in, for example, *Nerine* (e.g., Gouws, 1949) also probably indicate the presence of supernumerary chromosomes.

The only other previous count for the group, $2n = 22$ in *Strumaria truncata*, (Wilsenach, 1965) is not supported; two populations studied here had $2n = 20$, with karyotypes matching other species in the genus (Fig. 1B). In a third population individuals of S. *truncata* were found with $2n = 21$, the extra chromosome rather small and as in *H. zeyheri*, regarded as a B-chromosome. It seems likely that the karyotype described by Wilsenach consisted of $2n = 20 + 2B$, a suggestion supported by his illustration in which the 11th pair is much smaller than the others and almost telocentric.

As can be seen from the illustrations, the karyotypes of all four species of *Strumaria* and of three of the species of *Hessea*, *H. gemmata*, H. sp., and *H. chaplinii*, are all very similar (Figs. 1, 2A–C). This karyotype consists of a very long metacentric pair, four somewhat shorter ± submetacentric pairs, an acrocentric chromosome pair with a very large satellite much exceeding the shorter

TABLE 1. Chromosome number in *Strumaria*, *Hessea*, and *Carpolyza*. The following abbreviations are used: C.P. = Cape Province; S.W.A. = South West Africa.

Species	2*n*	Collection Data or Previous Count
Strumaria		
S. cf. *bidentata* Schinz.	20	S.W.A.; 15 km E of Witputs, *Tolken* 3989 (BOL).
S. *rubella* Jacq.	20	C.P.; 5 km N of van Rhynsdorp, N.B.G. expedition 171/65 (NBG).
S. truncata Jacq.	20	C.P.; 30 km W of Bitterfontein, Namaqualand, *Hall s.n.* (NBG). SW of Wildeperdehoek Pass, Namaqualand, *Hiemstra 493* (NBG).
	20, 20 + 1B	C.P.; Near Kamieskroon, Namaqualand, *Goldblatt* (MO, NBG).
	22	(Wilsenach, 1965).
S. sp.	20	C.P.; Top of van Rhyns Pass, *Tolken 4003* (BOL).
Hessea		
H. gemmata (Ker) B. & H.	20	C.P.; Soetmelksrivier, W of Albertinia, *Lewis 5915* (NBG).
H. sp.	20	C.P.; Droerivier, van Rhynsdorp dist., *Tolken 3997* (BOL).
H. chaplinii Barker	20	C.P.; Paternoster, Saldanha dist., *Thomas s.n.* (NBG).
H. tenella (L.f.) Oberm.	20	C.P.; Rondebosch Common, Cape Peninsula.
H. zeyheri Baker	22, 23(22 + 1B), 24 (22 + 2B)	C.P.; Spektakelberg Pass, Namaqualand, *Goldblatt 2018* (MO, NBG).
	24(22 + 2B), 25(22 + 3B)	C.P.; E of Pakhuis Pass, *Goldblatt 1849* (MO, NBG).
	24(22 + 2B)	C.P.; Near Bullshoek, Olifants River Valley, *Goldblatt*, no voucher.[a]
	24	(Wilsenach, 1965).
Carpolyza		
C. spiralis Salisb.	20	C.P.; Imhofs Gift, Cape Peninsula, *Esterhuysen 32612* (BOL). Cogmans Kloof, Montagu, *Goldblatt 2102* (MO). Rivierson-end, *Goldblatt 2054* (MO).

[a] Determination provisional, flowers not seen.

chromosome arm, and four shorter pairs. Size distinctions are not always clear cut, and chromosomes do grade in size. Nevertheless, this description represents the situation fairly accurately.

Hessea tenella has a similar karyotype except that the satellite is in a different position, on the second longest pair which is acrocentric (Fig. 2D).

Carpolyza also has a slightly different karotype; here the longest pair is acrocentric in contrast with the usually metacentric long pair. In other respects, including the large satellite on a small chromosome pair, the karyotype conforms to the general condition. The chromosomes of this species seem slightly smaller than in others but not to any significant degree (Fig. 2F).

The cytology of *Hessea zeyheri*, with diploid counts ranging from $2n = 22$–25, is all the more remarkable in view of the almost uniform pattern in the remainder of the species studied. The karyotype comprises three large ± acrocentric pairs,

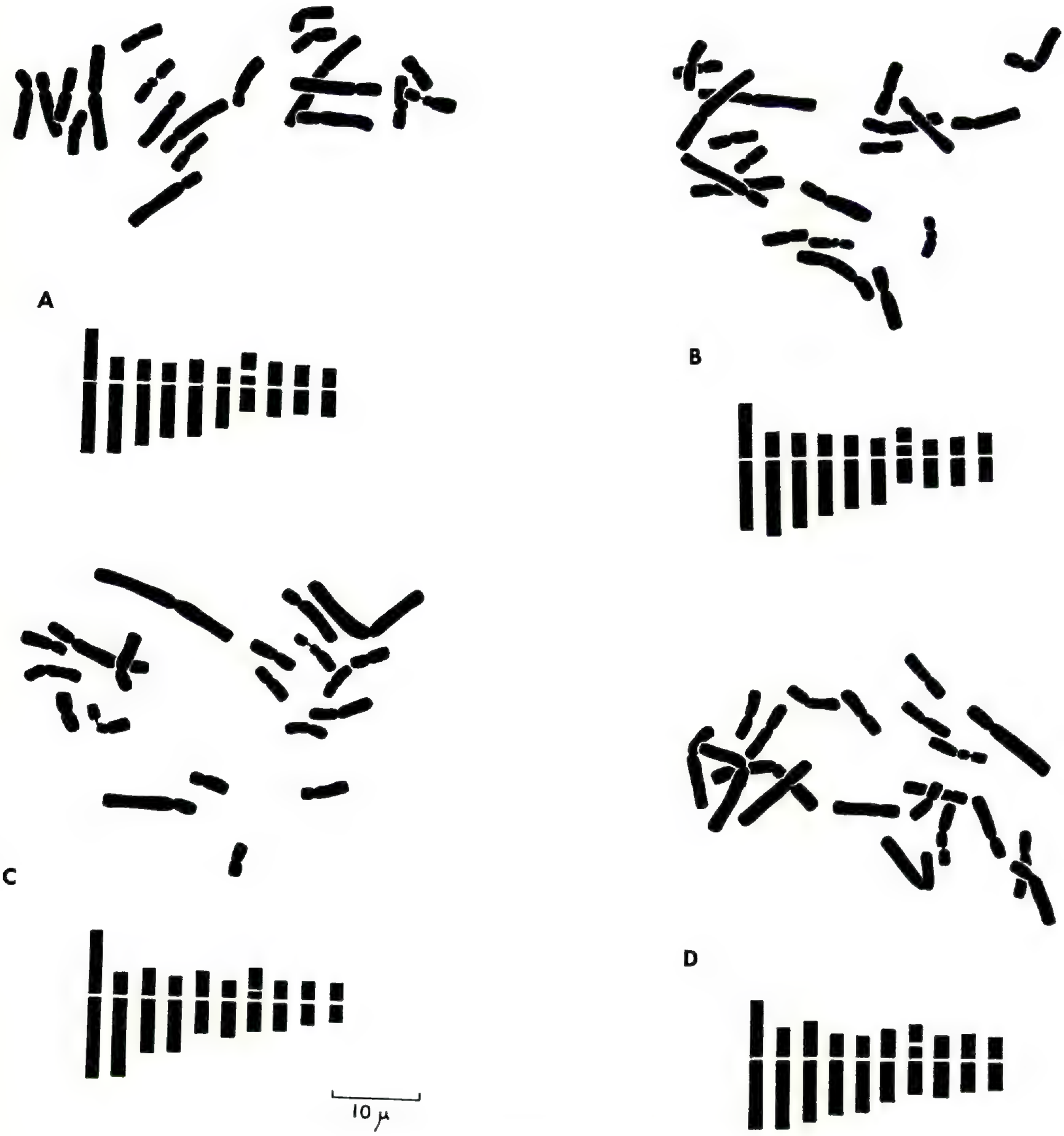

FIGURE 1. Mitotic metaphase and karyotypes in *Strumaria*.—A. *S. rubella*.—B. *S. truncata*.—C. *S.* sp.—D. *S.* cf. *bidentata*.

a fourth acrocentric pair with a very long satellite, and between 14 and 17 much smaller chromosomes mostly submetacentric but with telocentrics in cells with more than $2n = 22$. The basic number in this species is, as already suggested, probably $x = 11$, with a variable number of supernumerary, telocentric chromosomes occurring in many individuals.

The difference between the karyotype of this species and the more usual one in *Hessea* and *Strumaria*, apart from the supernumeraries, is that *H. zeyheri* has considerably more small chromosomes (Fig. 2E) while the other species have an extra two large chromosome pairs. The configuration of the chromosomes thus suggests the possible derivation of the more common $x = 10$ karyotype from the $x = 11$ condition in *Hessea zeyheri*, partly by Robertsonian translocation. Con-

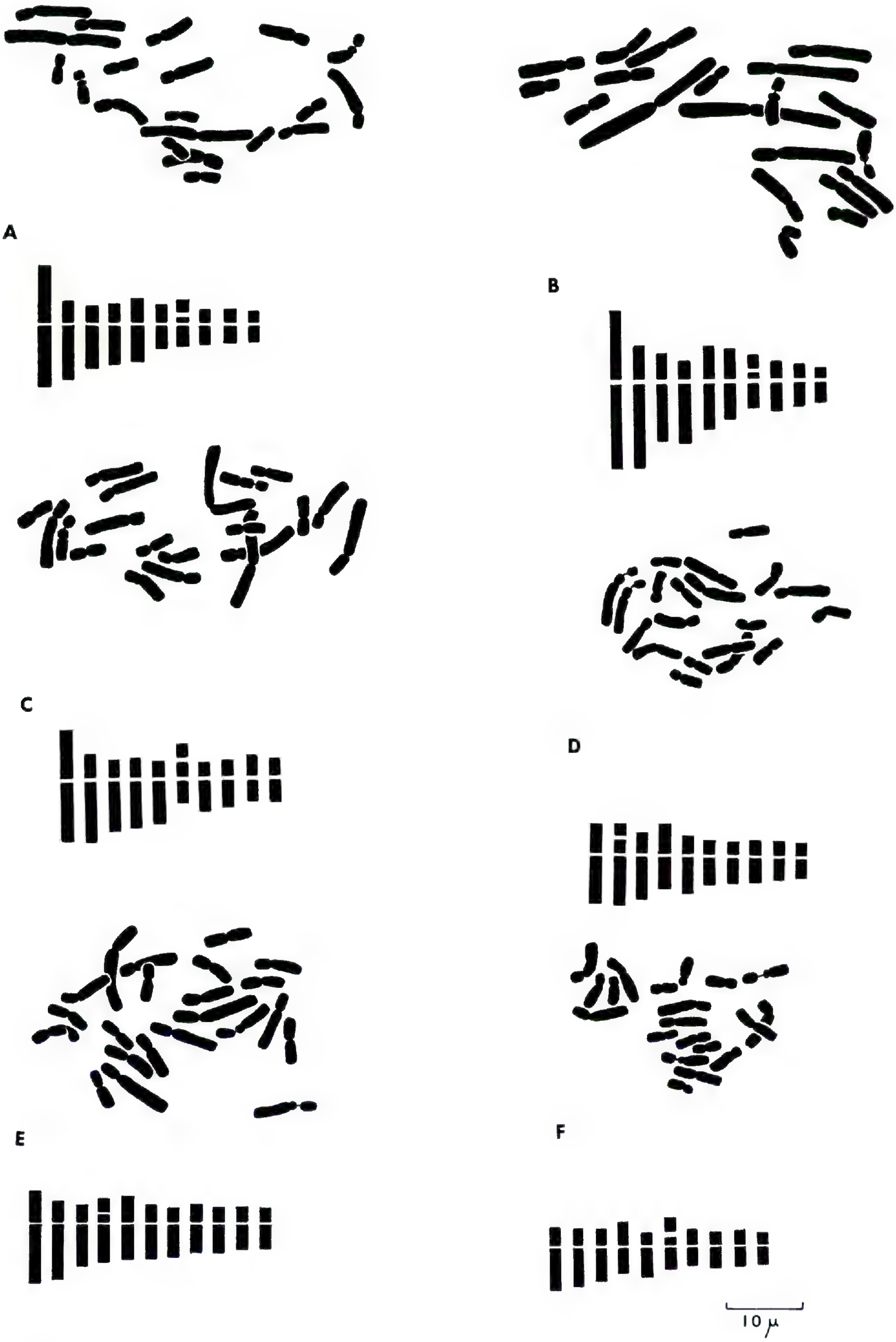

FIGURE 2. Mitotic metaphase in *Hessea* and *Carpolyza*.—A. *Hessea* sp.—B. *H. chaplinii*.—C. *H. gemmata*.—D. *H. tenella*.—E. *H. zeyheri*.—F. *Carpolyza spiralis*.

siderable chromosomal rearrangement is also indicated for the karyotype of *H. zeyheri* to approximate the condition in the other species examined. This suggestion assumes that reduction in number took place and there is some reason to believe that *H. zeyheri* is ancestral or primitive in the group, as discussed below.

Discussion

All species of *Hessea*, *Strumaria*, and *Carpolyza* are small plants with small flowers, and it seems likely that they are reduced relatives of the large group of Amaryllideae that evolved locally in parts of southern Africa under arid climatic conditions. With $x = 11$ almost certainly basic and fundamental in the tribe Amaryllideae, the *Strumaria-Hessea-Carpolyza* alliance, excluding *H. zeyheri*, seems a natural group with the reduced base number of $x = 10$. The exception which considerably complicates the situation is *H. zeyheri*: the possession of $x = 11$ in this species may represent a contradiction to the assumption that (a) the *Strumaria* alliance is a natural one, and (b) that $x = 10$ is basic in this group.

To answer the first query a survey of the important characteristics of the group is necessary. The name *Strumaria* alludes to the swollen style, which is possessed not only by species of *Strumaria*, but also by some species of *Hessea*. The typical style in Amaryllideae is filiform and the various elaborations possessed by *Strumaria* and some species of *Hessea* seem almost certainly derivative. Those species in the group with filiform styles might then be regarded as primitive. These include *Carpolyza*, as well as *Hessea zeyheri* and its close allies *H. stellaris* and *H. cinnamomea*. Notably, it is only in these few species that the tepals are united in a short tube and the stamens are epipetalous. United tepals and epipetalous stamens occur in most of the Amaryllideae, such as *Crinum*, *Ammocharis*, many species of *Brunsvigia*, and some species of *Nerine*, and this condition also is probably ancestral within the tribe.

This is morphological evidence supporting the suggestion that *Carpolyza* and the species of *Hessea* with filiform styles and short perianth tubes are primitive in the alliance. If this hypothesis is accepted, the higher base number in *Hessea zeyheri* can be viewed as ancestral, with the base number $x = 11$ being the same as that in the majority of genera of Amaryllideae. Cytological examination of further species of the alliance, especially those related to *H. zeyheri*, may establish some answers to the problem.

A reevaluation of the generic limits may also be called for since certain species of *Hessea* may be more closely related to *Strumaria* in possessing strumose styles, free tepals and stamens, and similar karyotypes. In view of the cytological evidence the traditional distinction between *Hessea* and *Strumaria*, fully outspread tepals and upright flowers as against subpatent tepals in ± pendulous flowers, may be less significant than stylar characteristics and the presence of a perianth tube, as Phillips (1951) infers.

Conclusion

Cytological results support the hypothesis that the *Hessea-Strumaria-Carpolyza* alliance comprises a natural group of species related to the tribe Amaryllideae. The group is envisaged as comprising morphologically reduced species specialized

for survival in the arid areas of southern Africa. The ancestral chromosome number is probably $x = 11$, found in all Amaryllideae and in *H. zeyheri*; other species of *Hessea* as well as *Carpolyza* and *Strumaria* all have a similar karyotype with $x = 10$ and are presumed to have evolved from a *H. zeyheri*-like ancestor by aneuploid reduction of the base number. The elaborations of the basic filiform style in *Strumaria* and many species of *Hessea* are seen as developments subsequent to the change in basic number. These adaptations set the two genera, which appear in need of redefinition, well apart from *Carpolyza*, which retains many features believed to be primitive in the alliance. *Carpolyza* appears to have followed a different evolutionary pathway from the remainder of the *Hessea-Strumaria* alliance, though probably from a common ancestor with $x = 10$.

LITERATURE CITED

DANDY, J. E. & F. R. FOSBERG. 1954. The type of *Amaryllis belladonna* L. Taxon 3: 231–232.

DYER, R. A. 1954. The Cape belladonna lily. Taxon 3: 72–74.

GOLDBLATT, P. 1972. Chromosome cytology in relation to classification in *Nerine* and *Brunsvigia* (Amaryllidaceae). J. S. African Bot. 38: 261–275.

GOUWS, J. B. 1949. Karyology of some South African Amaryllidaceae. Pl. Life 5: 54–81.

HERBERT, W. 1837. Amaryllidaceae. James Ridgeway and Sons, London.

HUTCHINSON, J. 1959. Families of Flowering Plants. Ed. 2. Vol. 1. Monocotyledons. Clarendon Press, Oxford.

JONES, K. & J. B. SMITH. 1967. Chromosome evolution in the genus *Crinum*. Caryologia 20: 163–179.

PAX, F. & K. HOFFMANN. 1930. Amaryllidaceae. *In* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien. Ed. 2., Vol. 15a: 391–430. Wilhelm Engelmann, Leipzig.

PHILLIPS, E. P. 1951. The Genera of South African Flowering Plants. Ed. 2. Government Printer, Pretoria.

SEALY, J. R. 1939. *Amaryllis* and *Hippeastrum*. Kew Bull. 1939: 49–68.

TRAUB, H. P. 1954. Typification of *Amaryllis belladonna* L. Taxon 3: 102–111.

———. 1963. The genera of Amaryllidaceae. American Plant Life Soc., La Jolla, California.

———. 1965. Addenda to Traub's "The Genera of Amaryllidaceae". Pl. Life 21: 88–89.

——— & H. N. MOLDENKE. 1949. Amaryllidaceae: Tribe Amarylleae. American Plant Life Soc., Stanford, California.

UPHOF, J. C. T. 1938. The history of nomenclature—*Amaryllis* (Linn.) Herb., and *Hippeastrum* (Herb.). Herbertia 5: 101–109.

WILSENACH, R. 1965. On the karyology and phylogeny of some genera of the Amaryllidaceae. Pl. Life 21: 82–88.

CHROMOSOME CYTOLOGY, POLLEN STRUCTURE, AND RELATIONSHIP OF *RETZIA CAPENSIS*[1]

PETER GOLDBLATT[2] AND RICHARD C. KEATING[3]

ABSTRACT

A chromosome number of $n = 12$ is reported for *Retzia capensis*, and the pollen is described based on SEM and TEM studies. It is tentatively concluded that the recognition of the monotypic family Retziaceae is warranted. The family's closest affinity is with the Loganiaceae.

Retzia capensis Thunb. is an unusual and striking member of the sclerophyll flora of the Cape region of South Africa. The genus is monotypic and its relationships are poorly known. It is a shrub with ericoid leaves and has a flower with a well-developed corolla tube, five epipetalous stamens, and a bicarpellate superior ovary. These characteristics place it among the less specialized of the tubiflorous group of families, but its correct relationships and family position remain unsettled. It is most frequently assigned to the Solanaceae or Loganiaceae, or is considered a separate family, but its relationships to these families remain unclear. A study of pollen structure and chromosome cytology has thus been made in the hope that this information may help in learning more about its phylogeny.

METHODS AND OBSERVATIONS

CYTOLOGY

Buds of *Retzia capensis* were fixed in the field in 3:1 ethanol-acetic acid and subsequently anthers were squashed in lacto-propionic orcein. A chromosome number of $n = 12$ was obtained.

POLLEN STRUCTURE

Pollen specimens were acetolyzed prior to electron microscopy. TEM specimens were embedded in Luft's Epon 6:4. After sectioning the grains were stained in uranyl acetate and lead citrate and photographed on a Hitachi HS-8 transmission microscope. SEM specimens were critical point dried from an ethanol-Freon series and then coated with gold to 250–300 Å. Photographs were prepared on a Cambridge Steroscan scanning electron microscope.

Pollen grains of *Retzia capensis* (Figs. 1–5) are spheroidal equatorially; circular to semiangular in polar view. The exine is microreticulate or microperforate-

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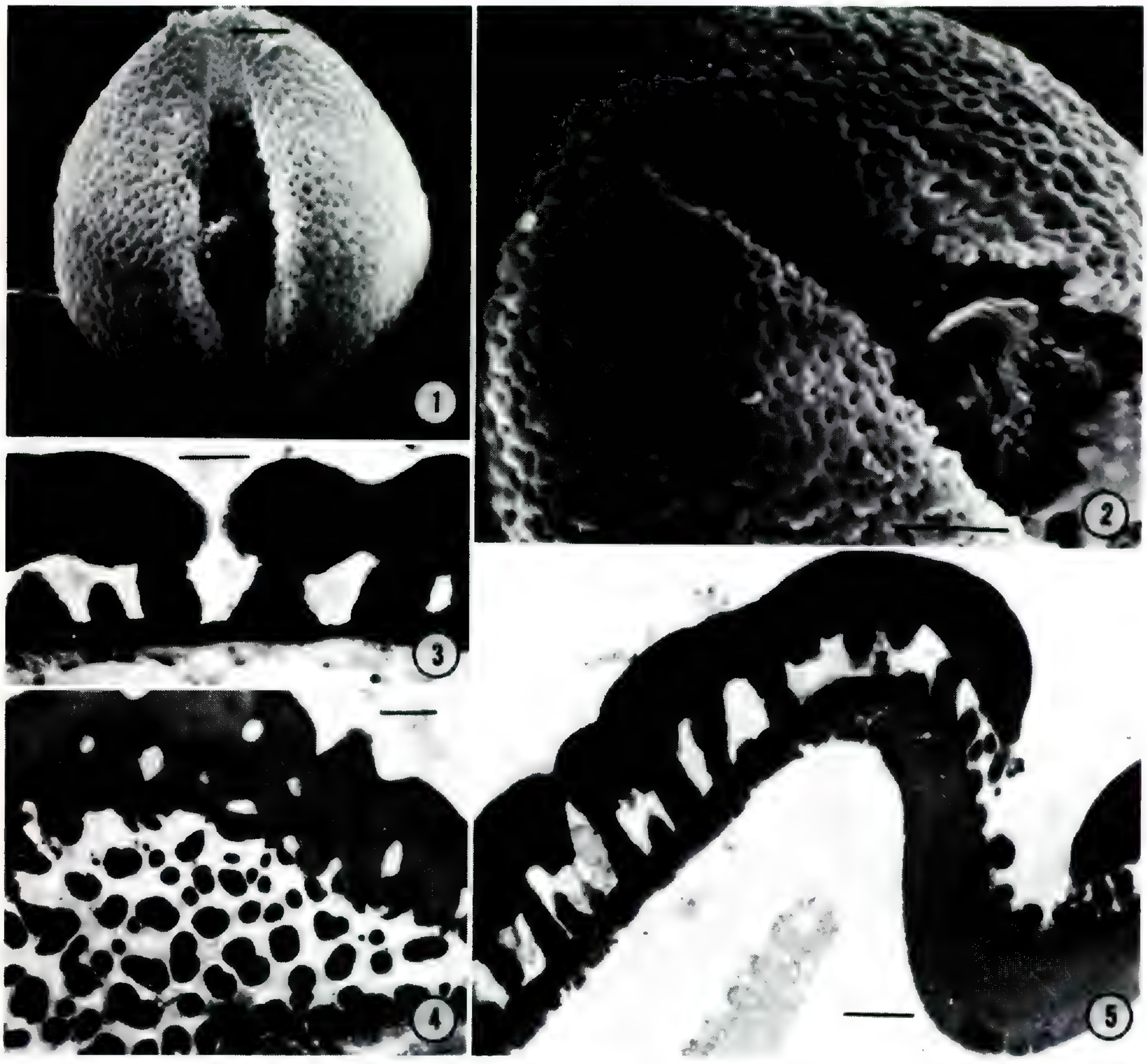
[4] Collection data for material used in this study: *Retzia capensis* Thunb. SOUTH AFRICA. CAPE: Near Bettys Bay, *Raven 21630* (voucher material at MO).



FIGURES 1–5. Pollen of *Retzia capensis*, SEM and TEM views.—1. SEM equatorial view of pollen grain with aperture. Scale line = 5 μm.—2. SEM oblique surface view of microreticulate exine. Note sculpturing elements on the colpus surface. Scale line = 5 μm.—3. TEM cross section of exine. Scale line = 1 μm.—4. TEM tangential section through exine. Note muri, lumina, and cross sections of baculae. Scale line = 1 μm.—5. TEM cross section of exine. Note thickened endexine layer under colpus and free sculpturing elements on the colpus surface. Scale line = 1 μm.

tectate with lumina narrower than muri. Lumina 0.3–0.8 μm; muri 0.8–1.8 μm. Exine thickness is 2.2–3.0 μm. Grains are tricolporate with an obscurely delimited endoaperture. Material exuding from endoaperatures of acetolyzed grains was occasionally seen (Fig. 2).

Muri are simpli-or duplibaculate due to very irregular width of the muri. A well-defined foot layer is clearly demarcated from the endexine. Tectum 1 μm, infratectal space 0.8–1.0 μm, foot layer 0.4–0.5 μm.

The thickness ratio of the tectum: infratectal space (columellae): foot layer is 2:2:1. The ecktexine: endexine ratio is 15:1. Columellae are circular or oblong in cross-section near their base and may become branched distally before attachment to the tectum. Costae (endexine) are 1.8 μm thick under the colpus.

Size of these specimens was E = 30 μm, P = 35 μm.

Discussion

The affinities of *Retzia* have long been a point of disagreement among botanists. Early treatments allied the genus to the Solanaceae, Polemoniaceae, or Convolvulaceae, but most modern works consider *Retzia* to be related either to the Solanaceae or Loganiaceae. Endlicher (1836) first placed it in the Solanaceae, as did de Candolle (1852) and Bentham & Hooker (1876), who assigned it to the solanaceous tribe Cestreae, close to *Sessea* and *Metternichia*. Lindley (1836) first proposed a relationship with Gentianales (Contortae) placing *Retzia* tentatively in Apocynaceae. Fedde (1896) seems to have been the first to suggest a specific relationship with Loganiaceae and this perhaps gained widest acceptance in recent times (Thonner, 1915; Leeuwenburg, 1964; Dahlgren, 1975), though Hutchinson (1969) still places *Retzia*, as a distinct family, in Solanales, while Takhtajan (1968) treats *Retzia* as a family in Scrophulariales, following Buddleiaceae.

An important contribution to the understanding of *Retzia* and its affinities was made by Fedde (1896) who studied the anatomy of Solanaceae in detail. Fedde concluded that *Retzia* was not allied to this family, as it lacked intraxylary (internal) phloem, a universal feature of Solanaceae, has pubescence of a different type, and is heavily cutinized, a feature unusual in Solanaceae. Fedde's results have recently been confirmed by Herbst (1972) whose detailed morphological and anatomical work is unfortunately unpublished.

Anatomically, *Retzia* seems somewhat better allied with the Loganiaceae-Buddleioideae, as this subfamily lacks the internal phloem characteristic of other groups of the Loganiaceae (Metcalfe & Chalk, 1950), while having comparable pubescence. Leeuwenberg (1964) admits a close affinity of *Retzia* with Buddleieae, but places it in a separate tribe. Herbst (1972) reaches a similar conclusion but prefers to retain separate family status for *Retzia*, placing it near Loganiaceae-Buddleioideae.

More recently, Jensen et al. (1975) have found important chemotaxonomic evidence relating *Retzia* to the limited group of orders which contain iridoid compounds. The orders in which iridoids occur include Gentianales and Scrophulariales, but notably not Solanales. Thus phytochemical data also points to the exclusion of *Retzia* from the Solanaceae. Unfortunately, the iridoid compound in *Retzia* has not been fully identified so that it is as yet not possible to use this chemical evidence for determining more detailed relationships of the genus.

The pollen structure, described by Punt & Leenhouts (1967), is confirmed, though we have noted a considerably smaller pollen size, 30×35 μm as compared to 43×45 μm. The unremarkable, tricolporate grains are quite unlike *Sessea* and *Metternichia*, the two genera of the Solanaceae with which *Retzia* has been allied, but according to Punt & Leenhouts (1967) exhibit a resemblance with certain groups in the Loganiaceae, notably Gelsemieae, and, to a lesser degree, Buddleioideae.

Against this background, the haploid chromosome number of $n = 12$ in *Retzia* provides disappointingly little information. The same number, $x = 12$, is probably basic in the Solanaceae (Raven, 1975), but this concurrence is presumably co-

incidental and more advanced members of this family, including the Cestreae to which *Retzia* has been allied, generally have lower base numbers.

Loganiaceae, which appears to be a very heterogeneous alliance, has a wide range of chromosome numbers, and natural groups within the family are often accorded tribal, subfamily, or even family status. Loganioideae, including Antonieae, Strychneae and Loganieae, apparently has $x = 22$ (also with $x = 20$ in the last mentioned); Spigelieae evidently $x = 8$, though with $n = 10$ in *Cynoctonium*; Gelsemieae also $x = 10$ and 8; and Potalieae $x = 6$, in *Fagraea* and *Anthocleista*. The distinctive Buddleioideae stand out as having $x = 19$, though only three of the approximately ten genera in the alliance have been studied. This incidentally lends support to suggestions that this group is only indistinctly allied to the Loganioideae and perhaps merits separate family status. A close relationship of *Retzia* and Buddleioideae seems unlikely in view of the distinctive base number in this group, even accepting the anatomical similarities.

The most likely ancestral base number for Loganiaceae is tentatively suggested as $x = 6$, found only in the relatively unspecialized primitive Potalieae. In this light, *Retzia* might be considered an ancestral tetraploid, derived in the distant past from basic loganiaceous stock and perhaps from a line leading to the Buddleioideae. A relationship with Loganiaceae also seems reasonable in phytogeographical terms, in view of the good representation of Loganiaceae in the Africa-Madagascar region in contrast with the poor development of Solanaceae in Africa, where, with the exception of *Cestrum*, possibly recently introduced, only members of the widespread Solaneae occur, a tribe which is not at all related to *Retzia*.

With the evidence currently available on the affinities of *Retzia capensis*, it is fairly clear that it is allied to Loganiaceae; however, the relationship is by no means close, nor is it possible to relate it to any particular group in this family. Thus it remains a highly subjective decision whether to include it in Loganiaceae, but the evidence does seem to favor separate family status as Retziaceae.

LITERATURE CITED

BENTHAM, G. & J. D. HOOKER. 1873. Genera Plantarum. Vol. 2. Reeve & Co., London.
CANDOLLE, A. DE. 1852. Prodromus Systematis Naturalis. Vol. 13. Masson, Paris.
DAHLGREN, R. 1975. A system of classification of the Angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119–147.
ENDLICHER, S. 1836. Genera Plantarum. Beck, Vienna.
FEDDE, F. 1896. Beiträge zur vergleichenden Anatomie der Solanaceae. Dissertation, Schreiber, Breslau.
HERBST, E. E. 1972. 'n Morphologiese ondersoek van *Retzia capensis* Thunb. Master's thesis, Univ. of Pretoria, Pretoria, South Africa.
HUTCHINSON, J. 1969. The Families of Flowering Plants. Vol. 1. Dicotyledons. Ed. 2. Clarendon Press, Oxford.
JENSEN, S. R., B. J. NIELSEN & R. DAHLGREN. 1975. Iridoid compounds, their occurrence and systematic importance in the Angiosperms. Bot. Not. 128: 148–180.
LEEUWENBERG, A. J. M. 1964. The Loganiaceae of Africa VI. *Retzia*. Acta Bot. Neerl. 13: 333–339.
LINDLEY, J. 1836. A Natural System of Botany. Ed. 2. Longman, London.
METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons. Vol. 2. Clarendon Press, Oxford.

PUNT, W. & P. W. LEENHOUTS. 1967. Pollen morphology and taxonomy in the Loganiaceae. Grana 7: 469–516.
RAVEN, P. H. 1975. The bases of angiosperm phylogeny: cytology. Ann. Missouri Bot. Gard. 62: 724–764.
TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Transl. by C. Jeffrey. Oliver and Boyd, Edinburgh.
THONNER, F. 1915. The Flowering Plants of Africa. Dulau & Co., London.

GENERIC AND SECTIONAL DELIMITATION IN ONAGRACEAE, TRIBE EPILOBIEAE[1]

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ABSTRACT

The available evidence is used to produce a revised taxonomy for Onagraceae tribe Epilobieae, with two genera, *Epilobium* and *Boisduvalia*. *Zauschneria* is a specialized, bird-pollinated taxon closely related to one group of *Epilobium*, and it is consequently reduced to the status of a section of that genus. It is treated as comprising a single species with three tetraploid ($n = 15$) and three octoploid ($n = 30$) subspecies, between which extensive intergradation occurs. *Chamerion* (*Chamaenerion*), a Eurasian group of seven species, two reaching North America, is closely related to and doubtless shares a common ancestor with *Epilobium* sect. *Epilobium*; the other four sections are more distantly related. They include a total of seven species, all xerophytes confined to western North America, the probable place of origin of the tribe. *Boisduvalia* is treated as comprising two sections in place of the three recognized earlier, based upon further morphological studies and evidence obtained from artificial hybridization. The taxonomy proposed for the tribe Epilobieae appears to provide a balanced classification for the group that brings it into line with the other five tribes and 15 genera of the family.

The tribe Epilobieae, with some 210 species, differs from the other five tribes in the family Onagraceae (Raven, 1964b) in its dotlike, almost entirely heteropycnotic chromosomes that persist as chromatic dots through interphase (Kurabayashi et al., 1962); basic chromosome numbers $x = 9$, 10, 12, 13, 15, 16, and 18; occurrence of many species in moist places; and, in all but a few species, the habit of shedding the mature pollen as tetrads. It may be related to the less specialized group Jussiaeeae, consisting of the genus *Ludwigia* (including *Jussiaea* and *Isnardia*), which resembles it in having dotlike, heteropycnotic chromosomes; in growing in moist places; and, in many species, in shedding its mature pollen in tetrads. The basic chromosome number of *Ludwigia*, however, is $x = 8$; its tetrads are made up of pollen grains that differ greatly from those of Epilobieae and have probably evolved independently (Skvarla et al., 1975); and it lacks interxylary phloem, present in Epilobieae (Carlquist, 1975). *Ludwigia* seems to be a relatively generalized genus within the family, resembling *Fuchsia* in its retention of primitive characteristics, as inferred by Eyde & Morgan (1973), and it probably is not directly related to Epilobieae, which then appear as a rather isolated group within the family. Although the fossil record is badly in need of reevaluation, Epilobieae probably extend back to Paleogene time (see discussion in Eyde & Morgan, 1973: 785).

Within this tribe, the genera are closely related to one another. This paper is directed to the following question: how many genera and sections, in the sense of Lewis & Lewis (1955) and Raven (e.g., 1963, 1969), is it useful to recognize?

Boisduvalia (Raven & Moore, 1965) includes six species of annual plants of western North and South America. Collectively, they are distinguished from

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Epilobium by their annual habit and lack of a coma, the tuft of long trichomes at the chalazal end of the seed that aids in dispersal. No species of *Epilobium* is both annual and lacks a coma, and no species is transitional between these two genera. In aspect, *Boisduvalia* is sharply distinct from *Epilobium*. Plants of *Boisduvalia* germinate in moist conditions, often actually submerged, and initially produce large, glabrous, opposite leaves similar to those of *Epilobium*. Later, they begin to produce alternate, sometimes densely pubescent, hard leaves, and when they produce flowers and fruits, they are often growing under decidedly xeric conditions. *Boisduvalia* includes two species with a gametic chromosome number of $n = 10$, one with $n = 9$, one with $n = 19$, and two with $n = 15$. The last is the only one of these chromosome numbers that also occurs in *Epilobium*; but, as we shall see, the species of these two genera with $n = 15$ seem to be unrelated.

As to the remainder of the tribe, the bird-pollinated, orange-red-flowered *Zauschneria*, comprising a single polytypic species of western North America, has been recognized as distinct since it was described by Presl in 1831. As early as 1806, Salisbury (1806: pl. 58), in describing *Chamaenerium halimifolium*, used the existence of *Zauschneria*, known to him from plants gathered by Archibald Menzies along the coast of northern California, as an argument for recognizing *Chamaenerion* as a genus distinct from *Epilobium*. *Zauschneria* was obviously generically distinct, yet had the coma of *Epilobium*: why not *Chamaenerion* also?

In fact, *Zauschneria* is more closely related to *Epilobium* sect. *Cordylophorum*, which I shall discuss below, than to *Epilobium* s. str. All species of both groups have a gametic chromosome number of $x = 15$, unique in *Epilobium* (Lewis & Raven, 1961); most have a relatively long floral tube; and all grow in xeric sites and are somewhat woody at the base. Their wood anatomy (Carlquist, 1975) is virtually identical. The single species of *Zauschneria* (see p. 335) shares with *Epilobium nevadense* and *E. nivium* a characteristic unusual for the tribe: a prominent apiculus of brown oil cells at the tip of each leaf (Brandegee, 1892; Stein, 1915; Munz, 1929; Raven, 1962a). Their seeds, like those of *Epilobium* sect. *Xerolobium* (comprising one highly polymorphic xerophytic annual species), are large, obovoid to clavate, and prominently constricted at the micropylar end (Seavey, Magill & Raven, 1977). Furthermore, *Zauschneria*, like *Boisduvalia* and the two sections of *Epilobium* just mentioned, as well as a third, *Epilobium* sect. *Crossostigma*, has large endexine channels in the distal pollen walls, which are therefore different from all other pollen walls in the family Onagraceae and a clear indication of relationship (Skvarla et al., 1976). The viscin threads in their pollen are thick and fluted (incised compound), unlike the less sharply ridged, tightly compound ones of sects. *Chamaenerion* and *Epilobium* (Skvarla et al., 1977). *Zauschneria* differs from the three species of *Epilobium* sect. *Cordylophorum* only in its longer floral tubes, orange-red flowers, and possession of a scale at the base of each stamen within the narrow part of the floral tube. These scales are highly variable and sometimes reduced to an irregular line (Curran, 1888). They appear to be homologous with the ring inside the floral tube in *Boisduvalia* (Curran, 1888: 255; Raven & Moore, 1965: 239, figs.

2–4) and in many species of *Epilobium*, such as *E. obcordatum* A. Gray. In the hummingbird-pollinated flowers of *Zauschneria*, this ring has apparently been somewhat elaborated during the course of evolution in relation to the protection of the abundant nectar from potential nectar thieves of low energetic requirements (Heinrich & Raven, 1972). *Zauschneria* is pollinated by hummingbirds and separated by the syndrome of characteristics typical of bird pollination from its bee-pollinated relatives, but overwhelmingly similar to them in all other respects.

The six species of *Boisduvalia* differ from all species of *Epilobium* in their distinctive seeds, which are irregularly angular-fusiform (Seavey, Magill & Raven, 1977). Furthermore, there is no indication that the ancestor of *Boisduvalia* possessed a coma. The development of a coma in the common ancestor of *Epilobium* and *Zauschneria* was an advance that delimits a demonstrably interrelated group of plants no more diverse than *Camissonia* (Raven, 1964b, 1969), *Fuchsia*, *Lopezia* (Eyde & Morgan, 1973; Plitmann et al., 1973) or *Ludwigia* (Raven, 1963). As early as 1888, Curran (1888: 255) suggested that *Zauschneria* probably should not be kept distinct from *Epilobium* at the generic level. Later Brandegee (1892), in his protologue for *Epilobium nivium*, indicated that this pattern of relationships clearly makes *Zauschneria* untenable as a taxon at the generic level, and I now propose to include it in *Epilobium* as a section.

Aside from *Zauschneria*, the only group within *Epilobium* as defined in this paper which has often been accorded generic status is *Chamerion* (*Chamaenerion*; Holub, 1972), comprising seven species of Eurasia, two of which (*E. angustifolium* L. and *E. latifolium* L.) extend into North America. In sect. *Chamaenerion*, the leaves are all spirally arranged—although cataphylls near the base of the shoots may be opposite in *E. latifolium*—and the flowers, being lateral instead of erect and terminal, are zygomorphic to varying degrees. The floral tube is obsolete, and the pollen is shed singly, not in tetrads.

It is mainly the large flowers and relatively large, hard leaves of sect. *Chamaenerion* which make it appear to be a distinctive group; yet *Epilobium rigidum* Hausskn. and, to a lesser extent, *E. obcordatum* A. Gray, two species of the western United States, undoubtedly belonging to sect. *Epilobium*, combine the large flowers and hard leaves of sect. *Chamaenerion* with actinomorphic flowers and a leaf arrangement that is initially opposite. It has not been doubted that these are "genuine" species of *Epilobium*; yet they suggest the sort of species of sect. *Epilobium* from which sect. *Chamaenerion* might have been derived. In both vegetative and floral characteristics, sect. *Chamaenerion* is specialized within the tribe Epilobieae, and in seeds (Seavey, Magill & Raven, 1977), pollen characteristics (Skvarla et al., 1976, 1977, unpublished), and chromosome number it resembles *Epilobium* s. str. (= sect. *Epilobium*) more closely than it does any other group. Furthermore, hybrids have been made between *E. glaberrimum* Barbey (sect. *Epilobium*; $n = 18$) and *E. angustifolium* (with $n = 36$; Mosquin, 1967), and other hybrids involving these two sections have likewise been made but not yet reported (G. Perraudin, personal communication). In view of all these facts, it seems certain that the obsolete floral tube, floral zygomorphy, unnotched petals, alternate leaves, and single pollen grains in *Chamaenerion* are derived from a

common ancestor with sect. *Epilobium*, its closest relative. As pointed out earlier, the recognition of *Chamerion* as a genus distinct from *Epilobium* would necessitate the separation of 4 other genera but still remove only 14 species from a genus with over 200 in all, and add several unfamiliar names in the process, while concealing the close relationship between all of these elements (Raven, 1962b). Recently, Holub (1972), without considering the generic balance in the family or any new facts, has reaffirmed the validity of this group at the generic level. His article is, in my opinion, nomenclaturally excellent but taxonomically not at all helpful.

Turning now to the more generalized and divergent species of *Epilobium*, there are three species, other than *Zauschneria*, with a gametic chromosome number of $n = 15$. Most similar to sect. *Zauschneria*, as pointed out by Brandegee (1892), is *E. nivium* T. S. Brandegee, a very local species of the north Coast Ranges of California, which has but two seeds in each locule of the capsule. This species, which can be regarded as a low, somewhat woody shrub, is interfertile with *E. nevadense* Munz (Seavey & Raven, 1977a) from the Charleston Mountains of southwestern Utah (Higgins, 1972), a spreading plant of loose scree in which there is only one seed in each locule of the capsule. Hybrids with the third species of *Epilobium* (other than *Zauschneria*) with $n = 15$, *E. suffruticosum* Nutt., have likewise been made experimentally (Seavey & Raven, 1977a), but have sharply reduced fertility despite their complete chromosome pairing. *Epilobium suffruticosum* grows along gravelly streams in the interior northwestern United States, and differs from the other two species to which it is related in having cream-colored, not rose-purple, petals, zygomorphic flowers, and many-seeded capsules.

The relationship between the annual *Epilobium paniculatum* Nutt. ex Torr. & A. Gray and the group consisting of *E. nivium* and *E. nevadense* was pointed out by Munz (1929) in his protologue for *E. nevadense*. *Epilobium paniculatum*, with *E. canum*, *E. nevadense*, and *E. nivium*, has a prominent apiculus consisting of brown oil cells (Stein, 1915) at each leaf apex. Oil cells are found in clusters on the leaves of many species of the family, but the apiculus in each of these four species is very similar and characteristic, strongly supporting the notion of a close relationship between them (Brandegee, 1892; Munz, 1929). In addition, *E. nevadense*, *E. nivium*, *E. suffruticosum*, and *E. paniculatum* resemble one another in that the petiole of the reduced leaf subtending each flower is fused with the pedicel so that the leaf appears to arise from the pedicel itself. This characteristic is known elsewhere in the genus only in *E. rigidum*, probably the least specialized species of sect. *Epilobium*, and a xerophyte like the other three. Whether the four species are directly related is uncertain but possible on the basis of other similarities. In *E. canum*, the subtending leaves are free of the pedicels, as in all other species of the genus. Since all three species of sect. *Cordylophorum* have the bract fused to the pedicel and *E. canum* does not, it may have been derived from their common ancestor and not from any existing species.

All strains of the very polymorphic *E. paniculatum* that we have examined have had a gametic chromosome number of $n = 12$; attempts to hybridize this species with *E. nevadense* have produced no results (Seavey & Raven, 1977b).

Nearly all populations of *E. paniculatum* consist of individuals that shed their mature pollen singly, a derived characteristic which they share with the species of sect. *Chamaenerion*; but we have recently discovered a few large-flowered populations in Siskiyou County, California, in which the mature pollen is shed in tetrads, and we intend to study these in more detail. Summing up, *Epilobium paniculatum* ($n = 12$) is a very distinct species, clearly related to sect. *Cordylophorum* ($n = 15$) and especially to *E. nevadense* and *E. nivium*; it seems to share at least one common ancestor with these other tetraploid species.

Remaining to be discussed are the other two annual species of *Epilobium* in addition to *E. paniculatum*: *E. minutum* Lindl. ex Lehm. ($n = 13$) and *E. foliosum* (Nutt. ex Torr. & A. Gray) Suksd. ($n = 16$). These two xerophytic annual species shed their pollen in tetrads and, despite their divergent chromosome numbers, are closely similar to one another and sometimes separable only with difficulty (Seavey, Wright & Raven, 1977). Their relationships within the genus are obscure, but they do have the large endexine channels in the distal walls of their pollen and incised-compound viscin threads (Skvarla et al., 1976, 1977) which negate a direct relationship with sects. *Epilobium* or *Chamaenerion*. In view of the absence of intermediate chromosome numbers, we have hypothesized that *E. minutum* and *E. foliosum* are probably derived independently from extinct diploid species with $n = 8$, 7, and 6; but the hypothesis cannot be verified until and unless such plants are discovered (Seavey, Wright & Raven, 1977).

Aside from the 14 species just discussed, which fall into five distinct groups, there are approximately 185 other species of *Epilobium* among which taxonomic subdivision is difficult if not impossible. Although there are some recognizable series among them, none is clearly defined. For example, the "creeping" species of New Zealand and adjacent islands, in which the flowers are borne laterally in the axils of leaves, all of which are opposite, whereas the terminal inflorescence is suppressed, appear distinctive. On closer examination, however, it can easily be seen (Raven & Raven, 1976), that these "creeping" species constitute a series of different lines that have acquired this habit independently; all hybridize readily with noncreeping species in the experimental garden, and some form natural hybrids also. Consequently, no clearly defined taxonomic group or groups can be separated among them, even though their presence is one of the things that imparts a distinctive aspect to the assemblage of *Epilobium* species found in New Zealand. It might be desirable to separate the species of *Epilobium* into series of the informal sort utilized by Haussknecht (1884), but intergrades between these series would then be so numerous that I consider their recognition, at least for the present, to be more confusing than helpful.

As to phylogenetic relationships within the tribe, I have already suggested that *Boisduvalia* separated before the evolution of a coma in the common ancestor of *Epilobium*. The common ancestor of the Epilobieae clearly had relatively large seeds (Seavey, Magill & Raven, 1977), large endexine channels in the distal walls of the pollen (Skvarla et al., 1976), incised-compound viscin threads (Skvarla et al., 1977), pollen in tetrads, a floral tube, actinomorphic flowers with a notch at the apex of each petal, lower leaves opposite, a perennial habit, anthers differentiated into two sets, a four-lobed stigma, and probably grew in dry places.

From this hypothetical common ancestor *Boisduvalia* was derived as an annual line, almost certainly in western North America, and in moist habitats. The original basic chromosome number in *Boisduvalia* seems to have been $n = 10$, judged both from the relationships within the group (Raven & Moore, 1965) and the fact that the original basic chromosome number for the family is clearly $n = 11$. From $n = 10$ was derived $n = 9$ [in *B. stricta* (A. Gray) Greene] and, indirectly, $n = 19$. Two closely related species of *Boisduvalia*, comprising sect. *Currania*, have $n = 15$, and are inferred to have been derived, probably from a common ancestor, following further aneuploid reduction below $n = 9$ and polyploidy; no species of Epilobieae with a gametic chromosome number less than $n = 9$ has survived to the present, however.

In *Epilobium* s. lat., the original basic chromosome number may have been $n = 9$. Kisch (1941) has shown that up to 9 bivalents, but also some multivalents, are formed in polyhaploids of *E. hirsutum* L. ($2n = 18$). From the basic number $n = 9$, sect. *Epilobium* and sect. *Chamaenerion* were derived by polyploidy, and may have been differentiated from a common ancestor with $n = 18$. Following Stebbins (1971: 193), I consider it likely that descending aneuploidy to $n = 6$ preceded the origin of the species with $n = 15$ ($9 + 6$?), $n = 16$ ($8 + 8$), $n = 13$ ($7 + 6$), and $n = 12$ ($6 + 6$). Our original hypothesis that $x = 6$ might be basic for *Epilobium* and the species with $n = 18$ hexaploid (Lewis et al., 1958) was formulated before the existence of species with $n = 16$, 15, and 13 was known. All four species of *Epilobium* with $n = 15$ ($n = 30$ also present in one) seem to have been derived from a common ancestor and, despite the present-day occurrence of *E. suffruticosum* in permanently moist places, this common ancestor seems to have been a xerophyte. Most of the extinct hypothetical diploids were also probably xerophytes, as implied by the xeric habitats of the three annuals with $n = 16$, 13, and 12. At any event, the common ancestor of *Epilobium* s. lat. clearly had a coma, as well as the other characteristics of the common ancestor of the tribe, and this innovation, which probably occurred in western North America, judged from present patterns of distribution, seems to have been the key to a worldwide distribution and proliferation into about 200 species. There seem to have been at least three independent evolutionary radiations into moist habitats: *Boisduvalia*, *Epilobium suffruticosum* (sect. *Cordylophorum*), and in *Epilobium* sect. *Epilobium*.

Synopsis of Onagraceae, Tribe Epilobieae

BOISDUVALIA

Boisduvalia Spach, Hist. Vég. Phan. 4: 383. 1835.

Oenothera sect. *Boisduvalia* (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 505, 1840.
Onothera group *Boisduvalia* (Spach) H. Lév., Monogr. Onoth. 296. 1908.
Cratericarpium Spach, Nouv. Ann. Mus. Hist. Nat. 4: 397. 1835. TYPE: *C. argyrophyllum* Spach = *Boisduvalia subulata* (Ruiz & Pav.) Raimann.

Annual herbs. Leaves subsessile, the lowest opposite. Flowers actinomorphic. Floral tube evident. Pollen shed in tetrads, the distal walls with large endexine channels. Viscin threads thick and incised-compound or smooth. Stigma 4-lobed,

clavate, or capitate. Seeds irregularly angular-fusiform, lacking a coma. Gametic chromosome numbers, $n = 10, 9, 19$, and 15.

Lectotype species: *B. concinna* (D. Don) Spach = *B. subulata* (Ruiz & Pav.) Raimann; Munz, Darwiniana 5: 126. 1941.

A recent monograph is that of Raven & Moore (1965).

1. **Boisduvalia** sect. **Boisduvalia.**

Oenothera sect. *Dictyopetalum* Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 45. 1835. TYPE: *B. concinna* (D. Don) Spach = *B. subulata* (Ruiz & Pav.) Raimann. *Boisduvalia* sect. *Dictyopetalum* (Fisch. & Mey.) Endl., Gen. Pl. 1191. 1840. *Boisduvalia* sect. *Euboisduvalia* Munz, Darwiniana 5: 127. 1941.

Oenothera sect. *Pachydium* Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 45. 1835. TYPE: *B. densiflora* (Lindl.) S. Wats. *Boisduvalia* sect. *Pachydium* (Fisch. & Mey.) Endl., Gen. Pl. 1191. 1840.

Mature leaves and stems villous or strigulose. Flowers usually chasmogamous. Stigma evidently to obscurely 4-lobed. Capsule terete, splitting to the base, the central column readily disintegrating or persistent. Seeds in one row in each locule or pushed together into a single row in the capsule by distortion of the median partition, nearly vertical. Gametic chromosome numbers, $n = 10, 9, 19$.

1. *Boisduvalia macrantha* Heller, Muhlenbergia 2: 101. 1905.
2. *Boisduvalia stricta* (A. Gray) Greene, Fl. Francisc. 225. 1891.
3. *Boisduvalia densiflora* (Lindl.) S. Wats., Bot. Calif. 1: 233. 1876.
4. *Boisduvalia subulata* (Ruiz & Pav.) Raimann, in Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 212. 1893.

The fact that the partitions between the locules in at least some strains of the South American *B. subulata* may be more persistent than those in the three North American species, used as a basis for sectional distinction earlier (Raven & Moore, 1965), no longer seems sufficient for separation. Seavey (unpublished) has obtained hybrids between *B. subulata* and the three other species of this section, and these show good association of chromosomes.

2. **Boisduvalia** sect. **Currania** Munz, Darwiniana 5: 127. 1941.

Mature leaves and stems sparsely pubescent or glabrous. Flowers usually cleistogamous. Stigma clavate, shallowly and irregularly 4-lobed. Capsule terete or sharply quadrangular, usually splitting only in the upper third, the central column readily disintegrating. Seeds in two rows in each locule, inclined about 20–60° from vertical. Gametic chromosome number, $n = 15$.

Lectotype species: *B. cleistogama* Curran; Raven & Moore, Brittonia 17: 251. 1965.

5. *Boisduvalia glabella* (Nutt.) Walp., Repert. Bot. Syst. 2: 89. 1843.
6. *Boisduvalia cleistogama* Curran, Bull. Calif. Acad. Sci. 1: 12. 1884.

EPILOBIUM

Epilobium L., Sp. Pl. 347. 1753; Gen. Pl., ed. 5. 164. 1754.

Chamaenerion Séguier, Pl. Veron. 3: 168. 1754; nom. illeg. LECTOTYPE: *Epilobium hirsutum* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion S. F. Gray, Natur. Arrang. Brit. Pl. 559. 1821; nom. illeg. TYPE: *C. spicatum* (Lam.) S. F. Gray = *Epilobium angustifolium* L.

Zauschneria Presl, Rel. Haenk. 2: 28, *pl.* 52. 1831. TYPE: *Z. californica* Presl = *E. canum* (Greene) Raven.

Chamerion (Raf.) Raf., Herb. Raf. 51. 1833. Based on *Epilobium* subg. *Chamerion* Raf., Amer. Monthly Mag. & Crit. Rev. 2: 266. 1818. TYPE: *E. amenum* Raf. = *E. angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion Spach, Hist. Nat. Veg. 4: 346. 1835; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Crossostigma Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 174. 1835. TYPE: *C. lindleyi* Spach, nom. illeg. = *E. minutum* Lindl. ex Lehm.

Chamaenerion Kostel, Ind. Pl. Hort. Bot. Prag. 34. 1844; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerium (Tausch) Schur, Sertum Fl. Transsilv. 25. 1853; nom. illeg. Based on *Epilobium* sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Pyrogennema Lunell, Amer. Midl. Naturalist 4: 482. 1916; nom. illeg. TYPE: *P. angustifolium* (L.) Lunell = *E. angustifolium* L.

Cordylophorum (Nutt. ex Torr. & A. Gray) Rydb., Fl. Rocky Mts. 590, 1064. 1917. Based on *Epilobium* sect. *Cordylophorum* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 488. 1840. TYPE: *C. suffruticosum* (Nutt.) Rydb. = *E. suffruticosum* Nutt.

Perennial herbs, often flowering the first year, with three species annual. Leaves petioled or sessile, the lowest opposite, or all alternate in sect. *Chamaenerion*. Flowers actinomorphic, zygomorphic in a few species. Floral tube evident, lacking in sect. *Chamaenerion*. Pollen shed in tetrads in all but a few species, the distal walls solid or with large endexine channels. Viscin threads thick, incised-compound; smooth; or tightly compound. Stigma 4-lobed, clavate, or capitate. Seeds variable, not angular, with a coma that has been lost in one species (*E. curtisiae* Raven) and a few strains of another (*E. ciliatum* Raf.). Gametic chromosome numbers, $n = 18, 16, 15, 13, 12$, and multiples of 18 and 15.

Lectotype species: *E. hirsutum* L.; Britton & Brown, Ill. Fl. No. U.S., ed. 2. 2: 590.

The only comprehensive monograph is that of Haussknecht (1884), but there have been recent accounts of the species of Europe (Raven, 1968), Turkey (Chamberlain & Raven, 1972), the *Flora Iranica* area (Raven, 1964a), the Himalayas (Raven, 1962b), Malesia (Raven, 1967a), Japan (Hara, 1942, 1965), Africa (Raven, 1967b), Australasia (Raven & Raven, 1976), North America (Munz, 1965), and South America (Samuelsson, 1923, 1930). A revised treatment of the species of North America is in progress.

1. **Epilobium** sect. **Cordylophorum** (Rydb.) Raven, stat. nov. Based on *Cordylophorum* Rydb., Fl. Rocky Mts. 590, 1064. 1917.

Clumped or rhizomatous perennial herbs. Basal, and in one species most, leaves opposite. Flowers actinomorphic or zygomorphic. Floral tube present, lacking scales within. Petals cream or rose purple, deeply notched. Pollen shed in tetrads, the distal walls of pollen with large endexine channels. Viscin threads thick, more or less incised-compound. Stigma deeply 4-lobed. Seeds large, obovoid to clavate, prominently constricted at the micropylar end. Gametic chromosome number $n = 15$.

Type species: *E. suffruticosum* Nutt.

1a. **Epilobium** sect. **Cordylophorum** subsect. **Nuttalia** Raven, subsect. nov.

Herbae perennes rhizomatosae. Folia plerumque opposita. Flores zygomorphi. Petala eburnea. Capsula seminibus multibus quoque locula. Semina clavata. Numerus chromosomaticus gameticus, $n = 15$.

Rhizomatous. Most leaves opposite. Flowers zygomorphic. Petals cream. Capsule with many seeds in each locule. Seeds clavate.

Type species: *E. suffruticosum* Nutt.

1. *Epilobium suffruticosum* Nutt., in Torr. & A. Gray, Fl. N. Amer. 1: 488. 1840.

Although morphologically distinctive, this species can be hybridized with *E. nevadense* and the chromosomes form 15 bivalents at meiotic metaphase I (Seavey & Raven, 1977a). It seems best to emphasize the similarities by retaining all three species within a single section.

1b. **Epilobium** sect. **Cordylophorum** subsect. **Petrolobium** Raven, subsect. nov.

Herbae perennes confertae ad basin sublingnosae. Folia basalia opposita. Flores actinomorphi. Petala roseo-purpurea, emarginata. Stigma profunde 4-lobatum. Pollen in tetradis effundatum. Capsula semina una vel dua quoque loculo. Semina obovoidea vel anguste obovoidea. Numerus chromosomaticus gameticus, $n = 15$.

Clumped. Basal leaves opposite. Flowers actinomorphic. Petals rose purple. Seeds one or two in each locule, obovoid or narrowly obovoid.

Type species: *E. nivium* T. S. Brandegee.

2. *Epilobium nivium* T. S. Brandegee, Zoe 3: 242, *pl. 24.* 1892.
3. *Epilobium nevadense* Munz, Bull. Torrey Bot. Club 56: 166. 1929.

2. **Epilobium** sect. **Xerolobium** Raven, sect. nov.

Herba annua erecta, saepe ad basin sublignosae; folia ad basin opposita, plerumque alternantia. Flores actinomorphi. Petala roseo-purpurea ad alba, emarginata. Stigma 4-lobatum ad integrum. Pollen plerumque singulariter effundata. Numerus chromosomaticus gameticus, $n = 12$.

Annual, xerophytic herb. Basal leaves opposite. Flowers actinomorphic. Floral tube present, lacking scales within. Petals rose purple or white, deeply notched. Stigma deeply 4-lobed to entire. Pollen shed singly in all but a few strains, the distal walls with large endexine channels. Viscin threads thick, incised-compound. Seeds obovoid, prominently constricted at the micropylar end. Gametic chromosome number, $n = 12$.

Type species: *E. paniculatum* Nutt. ex Torr. & A. Gray.

4. *Epilobium paniculatum* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 490. 1840.

This distinctive xerophytic annual seems to be closely related to the preceding species, but we have not yet succeeded in hybridizing it with them, and prefer to keep it distinct taxonomically. It is highly polymorphic but in a detailed study we have not found it useful to accord formal taxonomic recognition to any infraspecific units (Seavey & Raven, 1977b).

3. **Epilobium** sect. **Zauschneria** (Presl) Raven, stat. nov. Based on *Zauschneria* Presl, Rel. Haenk. 2: 28, *pl.* 52. 1831.

Clumped perennial, often woody at the base. Basal leaves opposite. Flowers zygomorphic, orange red. Floral tube elongate, with a scale at the base of each stamen, within the narrow part of the tube. Petals orange red, notched. Pollen shed in tetrads, the distal walls of pollen with large endexine channels. Viscin threads thick, incised-compound. Stigma deeply 4-lobed. Seeds obovoid, prominently constricted at the micropylar end. Gametic chromosome numbers, $n = 15, 30$.

Type species: *Zauschneria californica* Presl = *Epilobium canum* subsp. *angustifolium* (Keck) Raven.

5. **Epilobium canum** (Greene) Raven, comb. nov. Based on *Zauschneria cana* Greene, Pittonia 1: 28. 1887.

5a. **Epilobium canum** subsp. **septentrionale** (Keck) Raven, comb. nov. ($n = 15$). Based on *Zauschneria septentrionalis* Keck, Carnegie Inst. Wash. Publ. 520: 219. 1940.

5b. **Epilobium canum** subsp. **garrettii** (A. Nels.) Raven, comb. nov. ($n = 15$). Based on *Zauschneria garrettii* A. Nels., Proc. Biol. Soc. Wash. 20: 36. 1907.

5c. **Epilobium canum** subsp. **canum** ($n = 15$).

Zauschneria tomentella Greene, Pittonia 1: 25. 1887.

5d. **Epilobium canum** subsp. **angustifolium** (Keck) Raven, comb. nov. ($n = 30$). Based on *Zauschneria californica* subsp. *angustifolia* Keck, Carnegie Inst. Wash. Publ. 520: 221. 1940.

Zauschneria californica Presl, Rel. Haenk. 2: 28. 1831; Raven, Aliso 5: 215–216. 1962; non *Epilobium californicum* Hausskn., Monogr. Epil. 260. 1884.

5e. **Epilobium canum** subsp. **mexicanum** (Presl) Raven, comb. nov. ($n = 30$). Based on *Zauschneria mexicana* Presl, Rel. Haenk. 2: 29. 1831; non *Epilobium mexicanum* Moc. & Sessé ex DC., Prodr. 3: 41–1828.

Zauschneria villosa Greene, Pittonia 1: 27. 1887; non *Epilobium villosum* Thunb., Prodr. Fl. Cap. 75. 1794.
Zauschneria californica Presl subsp. *mexicana* (Presl) Raven, Aliso 5: 215. 1962.
Zauschneria californica Presl subsp. *typica* Keck, sensu Keck, Carnegie Inst. Wash. Publ. 520: 220. 1940. The type of Z. *californica* is, however, referable to the geographical race here called *Epilobium canum* subsp. *angustifolium* (Raven, Aliso 5: 215–216. 1962).

5f. **Epilobium canum** subsp. **latifolium** (Hook.) Raven, comb. nov. ($n = 30$). Based on *Zauschneria californica* var. *latifolia* Hook., Bot. Mag. *pl.* 4493. 1840.

Zauschneria latifolia (Hook.) Greene, Pittonia 1: 25. 1887.
Zauschneria californica subsp. *latifolia* (Hook.) Keck, Carnegie Inst. Wash. Publ. 520: 220. 1940.

Since the biosystematic revision of Keck (Clausen et al., 1940), it has been customary to regard this group as consisting of three species with a gametic

chromosome number of $n = 15$ and one with $n = 30$. Each of the entities with $n = 15$ intergrades with one of the entities with $n = 30$ to such an extent that separating them is often difficult or impossible, and autoploidy seems clearly to have been the mode in this complex (Clausen et al., 1940, 1945; Clausen, 1951). It has been suggested that the race here called *Epilobium canum* subsp. *mexicanum* has had, in effect, an alloploid origin following hybridization between the two other subspecies with $n = 30$, this again reemphasizing the close and dynamic relationship throughout the section. The complex seems fully comparable to *Eriophyllum lanatum* (Pursh) Forbes (Mooring, 1975), *Eriogonum fasciculatum* Benth. (Stebbins, 1971), *E. latifolium* Sm. (Stokes & Stebbins, 1955), *Haplopappus acradenius* (Greene) Blake (Stebbins, 1971), and *Artemisia tridentata* Nutt. (Ward, 1953), in which diploids or lower polyploids intergrade with their polyploid derivatives to such an extent that it is impossible to make a useful taxonomic separation. It is especially similar to the situation in *Dactylis glomerata* L., for which Stebbins & Zohary (1959) have suggested that a series of diploid, more or less interfertile, subspecies can best be accommodated in the same taxonomic species with their polyploid derivatives. Exchange of genetic material between diploids and polyploids must likewise be considered a serious possibility in a complex of this sort (cf. Müntzing, 1937, for *Dactylis*). In the light of these taxonomic considerations, it seems preferable to regard all entities recognized in *Epilobium* sect. *Zauschneria* as subspecies of a single polytypic species (Seavey & Raven, 1977a).

Only a partial synonymy is given here for this section; for further details consult Clausen et al. (1940), Tralau (1958), and Munz (1965).

4. **Epilobium** sect. **Crossostigma** (Spach) Raven, stat. nov. Based on *Crossostigma* Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 174. 1835.

Annual, xerophytic herbs. Basal leaves opposite. Flowers actinomorphic. Floral tube present. Petals pale rose purple or white, deeply notched. Pollen shed in tetrads, the distal walls of pollen with large endexine channels. Viscin threads thick, incised-compound or smooth. Stigma 4-lobed to subentire. Seeds obovoid. Gametic chromosome numbers, $n = 16, 13$.

Type species: *Crossostigma lindleyi* Spach = *Epilobium minutum* Lindl. ex Lehm.

6. *Epilobium foliosum* (Nutt. ex Torr. & A. Gray) Suksd., Deutsche Bot. Monatsschr. 18: 87. 1900.

7. *Epilobium minutum* Lindl. ex Lehm., in Hook., Fl. Bor-Amer. 1: 207. 1833.

The large endexine channels in the distal walls of the pollen and the incised-compound (or smooth) viscin threads (Skvarla et al., 1976, 1977) negate a possible relationship between these two reduced annual species and sect. *Epilobium*. *Epilobium foliosum* has been placed before *E. minutum* because it has evidently been derived from diploid ancestors with chromosome numbers closer to $n = 9$, the original basic chromosome number for the genus.

5. **Epilobium** sect. **Epilobium.**

Epilobium sect. *Lysimachion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *E. hirsutum* L.

Perennial herbs, mostly of moist places, often flowering the first year. Leaves opposite below, alternate above. Flowers actinomorphic. Floral tube present, lacking scales within. Petals rose purple or white, creamy in *E. luteum* Pursh, deeply notched. Pollen shed in tetrads, the distal walls with solid endexine. Viscin threads tightly compound. Stigma 4-lobed or entire. Seeds variable. Gametic chromosome number, $n = 18$.

This is a complex of approximately 185 species, found at high altitudes and high latitudes worldwide. Apparently all species can be hybridized. Judged by its seed morphology (Seavey, Magill & Raven, 1977), xeric habitat, large flowers, and 4-lobed stigma, *Epilobium rigidum* Hausskn. of the Siskiyou Mountains of northwestern California and southwestern Oregon may be the most generalized species, with *E. obcordatum* A. Gray, more widespread in the mountains of the western United States, related but more specialized. Curran (1888: 255) pointed out the similarity between the flowers of the latter and those of *Zauschneria* and *Boisduvalia.* Relationships within this section are highly reticulate, and it is not possible to suggest an overall arrangement with any confidence at this time, as discussed above.

6. **Epilobium** sect. **Chamaenerion** Tausch, Hort. Canal. fasc. 1. 1823.

Perennial herbs, occasionally somewhat woody near the base, of mesic habitats but usually not near water. Leaves alternate, the lowermost cataphylls often opposite in *E. latifolium* L. Flowers zygomorphic. Floral tube obsolete. Petals rose purple, entire. Stigma 4-lobed. Pollen shed singly, the distal walls with solid endexine. Viscin threads tightly compound. Seeds narrowly obovoid, smooth or papillose. Gametic chromosome numbers, $n = 18, 36, 54$.

Lectotype species: *E. angustifolium* L.

This distinctive assemblage is more closely related to sect. *Epilobium* than to any other group on the basis of hybridization experiments (Mosquin, 1967; G. Perraudin, personal communication), seed morphology (Seavey, Magill & Raven, 1977), pollen wall ultrastructure (Skvarla et al., 1976), viscin thread morphology (Skvarla et al., 1977), and chromosome number. It consists of two distinctive groups, for which subsectional rank seems appropriate.

6a. **Epilobium** sect. **Chamaenerion** subsect. **Rosmarinifolium** (T. Tacik) Raven, stat. nov. Based on *Chamaenerion* sect. *Rosmarinifolium* T. Tacik, in W. Szafer, Fl. Polska 8: 254. 1959.

Chamerion sect. *Rosmarinifolia* (T. Tacik) Holub, Folia Geobot. Phytotax. 7: 86. 1972.

Style pubescent in lower part. Seeds papillose. Gametic chromosome number, $n = 18$.

Type species: *Chamaenerion angustissimum* (Weber) Sosn. = *Epilobium dodonaei* Vill.

This subsection consists of four allopatric species of western Eurasia: *Epilobium colchicum* Alboff [including *E. caucasicum* (Hausskn.) Sosnowsky ex Grossheim], *E. dodonaei* Vill., *E. fleischeri* Hochst., and *E. stevenii* Boiss. All of these might conceivably be regarded as subspecies of a single polymorphic species, but that decision must wait further detailed study. Without such study, casual changes in taxonomic status such as those of Holub (1972) are without value: no reasons whatever were given. Natural hybrids between *E. dodonaei* and *E. fleischeri*, which replace one another altitudinally in the Alps, have been reported from time to time.

6b. **Epilobium** sect. **Chamaenerion** subsect. **Leiostylae** (Steinb.) Raven, stat. nov. Based on *Chamaenerium* sect. *Leiostylae* Steinb., Fl. U.S.S.R. 15: 626. 1949.

Chamaenerion Séguier, Pl. Veron. 3: 168. 1754; nom. illeg. LECTOTYPE: *Epilobium hirsutum* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Epilobium subg. *Chamerion* Raf., Amer. Monthly Mag. Crit. & Rev. 2: 266: 1818. TYPE: *E. amenum* Raf. = *E. angustifolium* L.

Chamerion S. F. Gray, Natur. Arrang. Brit. Pl. 559. 1821; nom. illeg. TYPE: *C. spicatum* (Lam.) S. F. Gray = *Epilobium angustifolium* L.

Epilobium sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *E. angustifolium* L.

Chamerion (Raf.) Raf., Herb. Raf. 51. 1833. Based on *Epilobium* subg. *Chamerion* Raf., Amer. Monthly Mag. Crit. & Rev. 2: 266. 1818. TYPE: *E. amenum* Raf. = *E. augustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion Spach, Hist. Nat. Veg. 4: 346. 1835; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion Kostel, Ind. Pl. Hort. Bot. Prag. 34. 1844; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerium (Tausch) Schur, Sertum Fl. Transsilv. 25. 1853; nom. illeg. Based on *Epilobium* sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerium sect. *Hebestylae* Steinb., Fl. U.S.S.R. 15: 622. 1949. LECTOTYPE: *Chamaenerium angustifolium* (L.) Scop. = *Epilobium angustifolium* L.

Chamaenerion sect. *Salicifolium* T. Tacik, in W. Szafer, Fl. Polska 8: 254. 1959. TYPE: *Chamaenerion angustifolium* (L.) Scop. = *Epilobium angustifolium* L.

Style pubescent in lower part or glabrous. Seeds smooth. Gametic chromosome numbers, $n = 18, 36, 54$.

Lectotype species: *Chamaenerium latifolium* (L.) Th. Fr. & Lange = *Epilobium latifolium* L.

This subsection includes three clearly delimited species: *Epilobium angustifolium* L. ($n = 18, 36, 54$; Mosquin, 1966), *E. latifolium* L. ($n = 18, 36$; Small, 1968), and *E. conspersum* Hausskn. The first-mentioned species is circumboreal (Mosquin, 1966), reaching northern Mexico (Munz, 1960) and Morocco (Dahlgren & Lassen, 1972); the second is circumpolar (Small, 1968); and the third is Himalayan (Raven, 1962b). The extent of natural hybridization between *E. angustifolium* and *E. latifolium* has been reviewed by Mosquin (1966: 184), and hybrids between these two species and *E. conspersum* have been mentioned by Raven (1962b). As pointed out by Dandy (1969), even if this group is treated

as generically distinct from *Epilobium*, it cannot take the name *Chamaenerion* which is an illegitimate substitute for *Epilobium*.

Literature Cited

Brandegee, T. S. 1892. A new *Epilobium*. Zoe 3: 242–243.

Carlquist, S. 1975. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon woods. Ann. Missouri Bot. Gard. 62: 386–424.

——— & P. H. Raven. 1966. The systematics and anatomy of *Gongylocarpus* (Onagraceae). Amer. J. Bot. 53: 378–390.

Chamberlain, D. F. & P. H. Raven. 1972. Onagraceae. *In* P. H. Davis (editor), Flora of Turkey. Vol. 4: 180–196. University Press, Edinburgh.

Clausen, J. 1951. Stages in the Evolution of Plant Species. Cornell Univ. Press, Ithaca, N.Y. viii + 206 pp.

———, D. D. Keck & W. M. Hiesey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Publ. Carnegie Inst. Wash. 520: i–vii, 1–452.

———, ——— & ———. 1945. Experimental studies on the nature of species. II. Plant evolution through amphiploidy and autoploidy, with examples from the Madiinae. Publ. Carnegie Inst. Wash. 546: i–vii, 1–174.

Curran, M. K. 1888. Botanical notes. Proc. Calif. Acad. Sci., ser. 2, 1: 227–269.

Dahlgren, R. & P. Lassen. 1972. Studies in the flora of northern Morocco. I. Some poor fen communities and notes on a number of northern and Atlantic plant species. Bot. Not. 125: 439–464.

Dandy, J. E. 1969. Nomenclatural changes in the *List of British Vascular Plants*. Watsonia 7: 157–178.

Eyde, R. H. & J. T. Morgan. 1973. Floral structure and evolution in Lopezieae (Onagraceae). Amer. J. Bot. 60: 771–787.

Hara, H. 1942. Preliminary study on Japanese *Epilobium*. J. Jap. Bot. 18: 173–186, 229–249.

———. 1965. *Epilobium*. Pp. 656–658, *in* J. Ohwi, Flora of Japan. Smithsonian Institution Press, Washington, D.C.

Haussknecht, C. 1884. Monographie der Gattung *Epilobium*. Gustav Fischer, Jena. viii + 318 pp. + 23 *pls.*

Heinrich, B. & P. H. Raven. 1972. Energetics and pollination ecology. Science 176: 597–602.

Higgins, L. C. 1972. Plants new to the Utah Flora. Great Basin Naturalist 32: 117–119.

Holub, J. 1972. Taxonomic and nomenclatural remarks on *Chamaenerion* auct. Folia Geobot. Phytotax. 7: 81–90.

Kisch, R. 1941. Morphologie und Zytologie haploider Pflanzen von *Epilobium hirsutum*. Z. Bot. 36: 513–537.

Kurabayashi, M., H. Lewis & P. H. Raven. 1962. A comparative study of mitosis in the Onagraceae. Amer. J. Bot. 49: 1003–1026.

Lewis, H. & M. E. Lewis. 1955. The genus *Clarkia*. Univ. Calif. Publ. Bot. 20: 241–392.

——— & P. H. Raven. 1961. Phylogeny of the Onagraceae. Pp. 1466–1468, *in* Recent Advances in Botany. Univ. Toronto Press, Toronto.

———, ———, C. S. Venkatesh & H. L. Wedberg. 1958. Observations of meiotic chromosomes in the Onagraceae. Aliso 4: 73–86.

Mooring, J. S. 1975. A cytogeographic study of *Eriophyllum lanatum* (Compositae, Helenieae). Amer. J. Bot. 62: 1027–1037.

Mosquin, T. 1966. A new taxonomy for *Epilobium angustifolium* L. (Onagraceae). Brittonia 18: 167–188.

———. 1967. Evidence for autopolyploidy in *Epilobium angustifolium* (Onagraceae). Evolution 21: 713–719.

Müntzing, A. 1937. The effects of chromosomal variation in *Dactylis*. Hereditas 23: 113–235.

Munz, P. A. 1929. New plants from Nevada. Bull. Torrey Bot. Club 56: 163–167.

———. 1960. North American species of *Epilobium* south of the United States. Aliso 4: 485–490.

———. 1965. Onagraceae. N. Amer. Fl., ser. 2, 5: 1–278.

PLITMANN, U., P. H. RAVEN & D. E. BREEDLOVE. 1973. The systematics of Lopezieae (Onagraceae). Ann. Missouri Bot. Gard. 60: 478–563.
RAVEN, P. H. 1962a. The systematics of *Oenothera* subgenus *Chylismia*. Univ. Calif. Publ. Bot. 34: 1–122.
———. 1962b. The genus *Epilobium* in the Himalayan region. Bull. Brit. Mus. (Nat. Hist.), Bot. 2: 325–382.
———. 1963. The Old World species of *Ludwigia* (including *Jussiaea*), with a synopsis of the genus (Onagraceae). Reinwardtia 6: 327–427.
———. 1964a. Onagraceae. *In* K. H. Rechinger (editor), Flora Iranica. Vol. 7: 1–19, *tab. 1–8*. Akademische Druck-u. Verlagsanstalt, Graz, Austria.
———. 1964b. The generic subdivision of Onagraceae, tribe Onagreae. Brittonia 16: 276–288.
———. 1967a. The genus *Epilobium* in Malesia (Onagraceae). Blumea 15: 269–282.
———. 1967b. A revision of the African species of *Epilobium* (Onagraceae). Bothalia 9: 309–333.
———. 1968. Onagraceae. *In* T. G. Tutin et al. (editors), Flora Europaea. Vol. 2: 305–311. Cambridge Univ. Press, Cambridge.
———. 1969. A revision of the genus *Camissonia* (Onagraceae). Contr. U.S. Natl. Herb. 37: 161–396.
——— & D. M. MOORE. 1965. A revision of *Boisduvalia* (Onagraceae). Brittonia 17: 238–254.
——— & T. E. RAVEN. 1976. The genus *Epilobium* (Onagraceae) in Australasia: a systematic and evolutionary study. New Zealand Dept. Sci. Indust. Res. Bull. 216: 1–321.
SALISBURY, R. A. 1806. Paradisus Londinensis. London. 117 pp. + *119 pls.*
SAMUELSSON, G. 1923. Revision der Südamerikanischen *Epilobium*-Arten. Svensk Bot. Tidskr. 17: 241–295.
———. 1930. Zur *Epilobium*-Flora Südamerikas. Svensk Bot. Tidskr. 24: 1–11.
SEAVEY, S. R. & P. H. RAVEN. 1977a. Experimental hybrids in *Epilobium* (including *Zauschneria*) species with $n = 15$ (Onagraceae). Amer. J. Bot. (in press).
——— & ———. 1977b. A new taxonomy for *Epilobium paniculatum* (Onagraceae). [In preparation.]
———, R. E. MAGILL & P. H. RAVEN. 1977. Evolution of seed size, shape, and surface architecture in the tribe Epilobieae (Onagraceae). Ann. Missouri Bot. Gard. (in press).
———, P. WRIGHT & P. H. RAVEN. 1977. A comparison of *Epilobium minutum* and *E. foliosum*. Madroño (in press).
SKVARLA, J. J., P. H. RAVEN & J. PRAGLOWSKI. 1975. The evolution of pollen tetrads in Onagraceae. Amer. J. Bot. 62: 6–35.
———, ——— & ———. 1976. Ultrastructural survey of Onagraceae pollen. *In* I. K. Ferguson & J. Muller (editors), The Evolutionary Significance of the Exine. Linnean Soc. Symp. Ser. 1: 447–479. Academic Press, New York.
———, ———, M. G. CHISSOE & M. SHARP. 1977. An ultrastructural study of viscin threads in Onagraceae pollen. Pollen & Spores (in press).
SMALL, E. 1968. The systematics of autopolyploidy in *Epilobium latifolium* (Onagraceae). Brittonia 20: 169–181.
STEBBINS, G. L. 1971. Chromosomal Evolution in Higher Plants. Addison-Wesley Publ. Co., Reading, Massachusetts. viii + 216 pp.
——— & D. ZOHARY. 1959. Cytogenetic and evolutionary studies in the genus *Dactylis*. I: Morphology, distribution, and interrelationships of the diploid subspecies. Univ. Calif. Publ. Bot. 31: 1–40.
STEIN, F. 1915. Über Ölkörper bei Oenotheraceen. Oesterr. Bot. Z. 65: 43–49.
STOKES, S. G. & G. L. STEBBINS. 1955. Chromosome numbers in the genus *Eriogonum*. Leafl. W. Bot. 7: 228–233.
TRALAU, H. 1958. On the distribution of the genus *Zauschneria*. Bot. Not. 111: 455–467.
WARD, G. H. 1953. *Artemisia*, section *Seriphidium*, in North America. Contr. Dudley Herb. 4: 155–205.

ADDITIONAL PANAMANIAN PASSIFLORACEAE[1]

Alwyn H. Gentry[2]

Abstract

Seven species of Passifloraceae, *Dilkea acuminata*, *Tetrastylis lobata*, *Passiflora tiliaefolia*, *P. costaricensis*, *P. capsularis*, *P. edulis*, and *P. arborea* are for the first time reported for Panama. *Dilkea* and *Tetrastylis* represent new generic reports. *Passiflora williamsii* is reduced to a variety, as *P. platyloba* Killip var. *williamsii* (Killip) A. Gentry, and recent collections of *P. pittieri* suggest that sect. *Cirrhipes* and *Dolichostema* may not be distinct.

Eight additional species of Passifloraceae have been collected in Panama since the *Flora of Panama* (Woodson & Schery, 1958) treatment of the family. These include representatives of two genera new to Panama. All of these species come from wet-forest areas of the country. In addition, a name change is proposed for one Panamanian species as additional collections of *P. williamsii* and *P. platyloba* indicate that the two are not specifically distinct.

The three Panamanian genera of Passifloraceae may be distinguished as follows:

a. Stamens 5, borne on a well-developed gynophore; sepals 5; petals 5 or lacking; tendril (if present) unbranched.
  b. Styles 4; anthers held to one side of flower, filaments united beyond the gynophore, only their tips free ..... *Tetrastylis*
  bb. Styles 3; anthers radially distributed, filaments free from their union with gynophore ..... *Passiflora*

aa. Stamens 8 or 10, borne on calyx floor, not on a gynophore; sepals 4; petals 4; tendrils (if present) usually divided at the tips ..... *Dilkea*

Dilkea acuminata Mast., Trans. Linn. Soc. 27: 628. 1871.

The genus *Dilkea* has been thought to be confined to the Amazon basin. However, several collections of *Dilkea* from eastern Panama and the Chocó of Colombia are now at hand. The four Panamanian collections are all from Santa Rita Ridge, Colón Province; three are in fruit and the fourth in flower. *Duke 15284*, collected 23 Feb. 1968, was described as a small shrub 5 feet high with orangish fruits. The ovoid acuminate fruit is slightly more than 7 cm long and about 3 cm wide. The leaves are oblanceolate-elliptic tapering to a cuneate base and acuminate apex. *Foster 1758*, collected 23 Apr. 1970 and described as a 4 m shrub with yellow fruit, has leaves in part oblanceolate-oblong (25–26 cm long and 9–9.5 cm wide) and in part oblong-elliptic (14 cm long and 7 cm wide). The single fruit examined is globose and 4 cm in diameter with a slight apical elongation. *Dressler 3936*, collected 7 Feb. 1971, is described as a vine 5 m tall, mostly cauliflorous, the flowers white, stigma yellow. This specimen has leaves oblanceolate to oblong-oblanceolate, 20–25 cm long, 6.5–9 cm wide, cuneate to attenuate at the base, long (2 cm) acuminate to apically rounded. The flowers

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[1] Unqualified references to Killip throughout this paper refer to that author's monumental monograph (The American species of Passifloraceae. Publ. Field Mus. Nat. Hist., Bot. Ser. 19: 1–613. 1938.).

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Ann. Missouri Bot. Gard. 63: 341–345. 1976.

have the calyx 3.2–3.5 cm long and the ovary is distinctly stipitate. The flower parts are in fours. *Croat & Porter 15298*, collected 9 Jul. 1971, was noted as having a lemon yellow fruit and sweet pulp and seeds. The specimen has tendrils and was probably a vine although habit was not noted by the collectors; the fruits are not preserved with the collection. Both Chocó collections [*Gentry & Aguirre 15318* from the Río Tigre east of Unguia near the base of the Serrania del Darién and *Duke & Idrobo 11254* (NY) from rain forest NW of Alto Curiche] are sterile. My collection was a shrubby vine and the Duke & Idrobo collection is described as a tendriliferous vine. These collections have oblanceolate, acute to acuminate leaves (one leaf reaches 30 cm long and 9 cm wide).

Specific identification of the isthmian plant remains tentative. The five *Dilkea* species recognized by Killip (represented by a total of fifteen collections) were separated by rather tenuous differences in shape and size of fruits and leaves. The Panamanian plants are clearly neither *D. parviflora* nor *D. retusa*. The ovoid, 7 cm fruit of *Duke 15284* indicates *D. johannesii* Barb. Rodr., previously known only from the Central Amazon basin. The globose fruit of *Foster 1758* indicates *D. acuminata* or *D. wallisii* Mast. The former, previously known only from Manaus, Brazil, has oblanceolate or oblong-oblanceolate leaves more than three times longer than wide; the latter, known from Amazonian Venezuela, Peru, and Brazil, has broadly ovate to oblong-oblanceolate leaves less than three times as long as wide. Both species have recently been reported from Amazonian Colombia (Killip, 1960; Holm-Nielson, 1974). Leaf variation in the Panamanian plants exceeds that of *D. acuminata* and *D. wallisii* combined.

Despite the variability of the Panamanian and Chocó collections, I am convinced they represent a single taxon. I have chosen to identify them with *D. acuminata* in part because that is the oldest epithet. If variability in this complex in Amazonia is as extensive as it appears to be in Panama, at least *D. johannesii* and perhaps also *D. wallisii* are likely to prove synonymous with *D. acuminata*.

Tetrastylis lobata Killip, J. Wash. Acad. Sci. 16: 368. 1926.

Another genus of Passifloraceae which is new to Panama is *Tetrastylis*, represented by a single collection of *T. lobata* from Bocas del Toro Province. The collection (*Gentry 2808*) is from a recently cleared area in the valley behind the first fila above Almirante, Bocas del Toro Province and my field notes describe it as a herbaceous vine with white flowers and sticky leaves. *Tetrastylis* is easily told from *Passiflora* by its four styles and the arrangement of its stamens which are all held to one side of the gynophore rather than distributed evenly around it. The species is known from Costa Rica so its occurrence in Panama is hardly surprising.

Passiflora platyloba Killip var. **williamsii** (Killip) A. Gentry, stat. et comb. nov.

P. williamsii Killip, J. Wash. Acad. Sci. 12: 262. 1922.

Passiflora platyloba and *P. williamsii* were simultaneously published by Killip. The leaves glabrous beneath and deeply cordate in *P. platyloba* of Guatemala to Costa Rica (to Panama fide Killip, 1938: 59) were contrasted with leaves

puberulous and basally truncate or subcordate in *P. williamsii* of central Panama. Later Killip noted that the leaves of *P. williamsii* could also be cordate and emphasized its densely white tomentose ovary in separating it from *P. platyloba* in his monograph. Additional collections indicate the inconstancy of these differences. *Lewis et al. 2250* from Los Santos Province, Panama has the pubescent ovary and truncate leaves of *P. williamsii* but the leaves are only subpuberulous. *Duke 15516* from Darién Province has a puberulous ovary and puberulous leaves which are strongly cordate. *Heithaus 157* from COMELCO E (west of Bagaces), Guanacaste, Costa Rica has a glabrous ovary and cordate leaves with subpuberulous main veins beneath; *Gentry 838* from the same area has completely glabrous leaves. *Semple 69* from the same locality has completely glabrous leaves but was identified as *P. williamsii*. Since leaf variation is not geographically correlated, only ovary pubescence remains a potential character for segregation of the Panamanian from the Costa Rican and Central American plants. I do not consider this sufficient difference for species recognition. *Passiflora platyloba* is the best-known name and should be adopted for the Panamanian plants; indeed that name has already been used on some Panamanian collections in the Missouri Botanical Garden (MO) herbarium. Plants with pubescent ovaries are best recognized as *P. platyloba* var. *williamsii*.

Passiflora velata Mast. and *P. nitens* Johnston are similar variants of the closely related South American *P. serrulata* Jacq. which are separated only by indumentum of the leaf undersurface. Killip has already synonymized these with *P. serrulata*.

Passiflora tiliaefolia L., Sp. Pl. 956. 1753.

Passiflora tiliaefolia is a member of subgen. *Granadilla*, ser. *Tiliaefoliae* and has recently been collected in Panama. The collection (*Croat 25908* from above Santa Fe (730–770 m), Veraguas Province) resembles *P. seemannii* Griseb. in having large foliaceous bracts, glands at the petiole apex, and broadly ovate subentire leaves. It differs from that species in a very shallowly cordate leaf base and broader (ca. 5 mm wide), lanceolate foliaceous stipules. *Passiflora seemannii* has deeply cordate leaves with the lobes overlapping and linear stipules. Another difference between *P. tiliaefolia* and *P. seemannii* is the latter's tuberculate inner side of the calyx tube. The flowers of the Croat collection are immature; however, the operculum appears to be entire like *P. seemannii* but unlike the even more closely related *P. nelsonii* Mast. & Rose of Guatemala and southern Mexico.

Passiflora tiliaefolia was previously known from Peru to Colombia. It is widespread in the western and central cordilleras of Colombia and its occurrence in Panama is not especially surprising.

Passiflora costaricensis Killip, J. Wash. Acad. Sci. 12: 257. 1922.

A Central American species ranging from Guatemala to Costa Rica, the occurrence of *P. costaricensis* in Panama is almost to be expected. The species turns out to be widespread, though uncommon, in wet-forest areas throughout the country, having been collected in Bocas del Toro (above Almirante, *Gentry*

2690), Panamá (Cerro Campana, *Kennedy et al. 2054*), and Colón (Río Guanche, *Kennedy & Foster 2202*) Provinces. It can immediately be told from all other Panamanian species by its elongate fusiform fruit. In the *Flora of Panama* it keys out with *P. sexflora* which differs in several-flowered peduncles, small spherical fruits, smaller leaves, and a finer pubescence. *Passiflora costaricensis* is barely distinguishable from *P. capsularis* (see below) by its hirsute pubescence and the leaves longer than broad and with a semicircular sinus.

Passiflora capsularis L., Sp. Pl. 957, 1753.

This widespread species has been known from Guatemala to Costa Rica, Colombia, the Greater Antilles, and from Central Brazil to Paraguay. The unusual disjunctions in its range are suspect and, predictably, the species has turned up in Panama. The single Panamanian collection is *Duke & Lallathin 15023* from El Valle, Coclé Province. *Gentry 10211* and *Dodson 5240* (Selby) (both from the Río Palenque Field Station, Los Ríos Province) are the first Ecuadorean collections and partially fill another gap in the known range of the species, which is likely to be found in Peru as well. *Passiflora capsularis* keys out with *P. sexflora* in the *Flora of Panama* but differs in 1-flowered peduncles, elongate fusiform fruits, and less dense pubescence. Leaf shape and the shorter, often more or less appressed trichomes of the stem and petioles differentiate this species from *P. costaricensis*.

Passiflora edulis Sims, Bot. Mag. 45, *pl. 1989*. 1818.

The native range of this widely cultivated species is obscure but is probably Brazil. In Panama it is found in cultivation and semicultivation and occasionally as an escape. Panamanian collections include *Semple 30* and *Croat 14268* (both El Valle, Coclé Province) and *Tyson 5797* (Cerro Punta, Chiriquí Province). At least the Tyson collection was apparently growing wild. This species keys out with *P. adenopoda* Dc. and *P. vitifolia* H.B.K. in the *Flora of Panama* treatment. It agrees with the former in prominent petiolar glands borne directly beneath the leaf blade, serrate involucral bracts, and purple and white flowers. It agrees with the latter in 3-lobed leaves and sessile nonstipitate petiolar glands. Panamanian collections of *P. edulis* have been identified with both these species.

Passiflora arborea Spreng., Syst. Veg. 3: 42. 1826.

This tree *Passiflora* was previously known only from Colombia where it is fairly widespread. Two Panamanian collections, one in fruit and one sterile, match Colombian material and a photograph of the type of this species at MO and may be confidently referred to it. The Panamanian collections, from opposite ends of the country, are *Gentry & Mori 13800* from 1,400–1,500 m on Cerro Malí, Darién Province and *Kirkbride & Duke 730* from the headwaters of Río Malí, Chiriquí Trail, Bocas del Toro Province. My collection was a 3 m tree and the Kirkbride and Duke collection reportedly a 15 m tree. *Passiflora arborea* is utterly unlike any species listed in the *Flora of Panama* and is characterized by its arboreal habit, 3-angled ovary, long, bifurcate peduncle, and large (to 30 cm long and 19 cm wide) entire, pinnately veined oblong to elliptic-oblong leaves.

Passiflora pittieri Mast., Bot. Gaz. (Crawfordsville) 23: 246. 1897.

This species, like *P. arborea* a member of subgen. *Astrophea*, was described from Costa Rica and reported for Panama by Killip (1960) subsequent to the *Flora of Panama* treatment. In addition to the two Panamanian specimens cited by Killip (from Isla de Coiba and Pinogana, Darién) may now be added a third and very noteworthy collection. *Liesner 197* from San Bartolo Limite, 400–500 m, 12 mi W of Puerto Armuelles, Burica Peninsula, Chiriquí Province is described as petals white, calyx pale with brownish spots, column red, ovary and anthers greenish white. Although agreeing in most features, including the definitive long-tubular operculum, with *P. pittieri*, the dichotomously branched peduncles of the Liesner collection bear well-developed tendrils as in Killip's monotypic section *Cirrhipes*. Hence it appears that sects. *Cirrhipes* and *Dolichostemma* of subgen. *Astrophea* cannot be separated.

Another recent collection of *P. pittieri* is the first record of the species from Colombia's Chocó Department. *Gentry & Mori 13728* from near the Panamanian border at 1,000 m on the trail from Unguia to Cerro Malí is a sterile juvenile plant with axillary tendrils at the upper nodes. Allowing for its juvenile condition, it agrees fairly well with *P. pittieri* and is certainly none of the other species known from Panama.

Similar to *P. arborea* in large, entire, oblong-obovate leaves with glands at base of the midvein, bifurcate peduncles, and 3-angled ovary, *P. pittieri* differs from that species in its long-tubular operculum, tendency to lianous habit and (sometimes) tendrillate inflorescences.

Literature Cited

Holm-Nielsen, L. B. 1974. Notes on central Andean Passifloraceae. Bot. Not. 127: 338–351.

Killip, E. P. 1938. The American species of Passifloraceae. Publ. Field Mus. Nat. Hist., Bot. Ser. 19: 1–613.

———. 1960. Supplemental notes on the American species of Passifloraceae with descriptions of new species. Contr. U.S. Natl. Herb. 35: 1–23.

Woodson, R. E. Jr. & R. W. Schery. 1958. Passifloraceae. *In* Flora of Panama. Ann. Missouri Bot. Gard. 45: 1–22.

THE PANAMANIAN SPECIES OF *BAUHINIA* (LEGUMINOSAE)[1]

RICHARD P. WUNDERLIN[2]

ABSTRACT

Eleven species of *Bauhinia* native to Panama are enumerated with the three species new to the flora described. Synonyms, typification, and key to species are provided.

Twenty-five years have passed since the treatment of *Bauhinia* in the Flora of Panama appeared (Schery, 1951). It seems appropriate at this time to reassess the genus in light of studies that have taken place in the intervening years.

Schery recognized thirteen native plus two introduced Asiatic species (*B. purpurea* and *B. monandra*) for the flora of Panama. Eleven native species are recognized and discussed here.

Although at first it appears as if only a minor change has taken place, a decrease in two species, there is a significant modification in taxonomy and nomenclature. Actually, of the thirteen names employed by Schery, only four are retained here. Three species are added to the flora while five are reduced to synonymy. All other changes are nomenclatural.

Approximately 300 herbarium specimens of Panamanian materials from the following herbaria were examined for this study: DUKE, F, MO, NY, P, UC, USF, and US. The reader is referred to annotated specimens deposited in these herbaria. Annotated specimens of species discussed here but collected outside Panama are deposited in the following additional herbaria: A, COL, GH, IJ, ILL, K, MICH, SIU, TEX, UCWI, VT, W, and WIS. The author also had the opportunity to study six of the species in the field in Panama or elsewhere in the Neotropics: *B. aculeata*, *B. glabra*, *B. guianensis*, *B. pauletia*, *B. reflexa*, and *B. ungulata*.

BAUHINIA

Bauhinia L., Sp. Pl. 374. 1753, non Kunth, 1824, nec Raf., 1838. TYPE: *B. divaricata* L.

Pauletia Cav., Icon. Descr. Pl. 5: 5. 1799. LECTOTYPE: *P. inermis* Cav.
Amaria Mutis, Sem. Nuev. Rey. Gran. 2: 25. 1810. LECTOTYPE: *A. petiolata* Mutis ex DC.
Schnella Raddi, Mem. Soc. Ital. Modena 18: 411. 1820. LECTOTYPE: S. *macrostachya* Raddi.
Lacara Spreng., Neue Entdeck. 3: 56. 1822, non Raf., 1836. TYPE: *L. triplinervia* Spreng.
Bauhinia Kunth, Ann. Sci. Nat. (Paris) 1: 85. 1824, non L., 1753, nec Raf., 1838. LECTOTYPE: *B. aculeata* L.
Casparia Kunth, Ann. Sci. Nat. (Paris) 1: 85. 1824. TYPE: *C. pes-caprae* (Cav.) H.B.K.
Caulotretus Rich. ex Schott in Spreng., Syst. Veg., ed. 16. 4(2): 406. 1827. TYPE: *C. smilacinus* Schott.

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Perlebia Mart. in Spix & Mart., Reise Bras. 2: 555. 1828, non DC., 1829. TYPE: *P. bauhinioides* Mart.
Bauhinia Raf., Sylva Tell. 121. 1838, non L., 1753, nec Kunth, 1824. LECTOTYPE: *B. aculeata* L.
Binaria Raf., Sylva Tell. 121. 1838. TYPE: *B. cumanensis* (H.B.K.) Raf.
Cansenia Raf., Sylva Tell. 122. 1838. LECTOTYPE: *C. ungulata* (L.) Raf.
Mandarus Raf., Sylva Tell. 122. 1838. LECTOTYPE: *M. divaricatus* (L.) Raf.
Ariaria C. Marq., Estud. Arq. Etno. Amer. 1: 141. 1920. TYPE: *A. superba* C. Marq.

Other synonyms occur for *Bauhinia*. Only those which apply to Neotropical material are listed here. See Wunderlin (1975) for a complete synonymy and discussion of typification.

Key to the Native Panamanian Species of *Bauhinia*

a. Trees or shrubs with or without spines.
  b. Plants armed with intrastipular spines.
    c. Petals white, elliptic to obovate; fertile stamens 10; buds linear-lanceolate, 3–4(–5.5) cm long ..... 1. *B. aculeata*
    cc. Petals green, filiform; fertile stamens 5; buds filiform, 8–10(–12) cm long ..... 2. *B. pauletia*
  bb. Plants unarmed.
    d. Calyx limb splitting to hypanthium into several lobes.
      e. Petal blades ovate-elliptic, white to pinkish with roseate center; fertile stamens 8, other 2 reduced to a ligule ..... 3. *B. picta*
      ee. Petal blades filiform or linear, white; fertile stamens 10 ..... 4. *B. ungulata*
    dd. Calyx limb spathaceous.
      f. Shorter alternate stamens connate for about ½ their length; inner pair of leaf nerves closer to midrib than to adjacent nerves ..... 5. *B. bequinotii*
      ff. All stamens free nearly to base; inner pair of leaf nerves equi-distant or closer to adjacent nerves than to the midvein ..... 6. *B. petiolata*
aa. Tendriled vines or lianas.
  g. Calyx 5-nerved or inconspicuously nerved; fruit indehiscent, thin walled ..... 7. *B. microstacha*
  gg. Calyx conspicuously 10–15-nerved; fruit dehiscent, woody.
    h. Leaves shallowly to deeply cleft on mature plants, frequently bifoliolate on young plants; calyx about 1 cm long.
      i. Calyx lobes setaceous; pubescence various, but never with coppery sheen.
        j. Calyx lobes erect; petals pink or white, one with conspicuous purple spots ..... 8. *B. glabra*
        jj. Calyx lobes reflexed; petals pink, without markings ..... 9. *B. reflexa*
      ii. Calyx lobes ovate to lanceolate or sometimes nearly absent; young parts of plants often with a coppery pubesence ..... 10. *B. guianensis*
    hh. Leaves bifoliolate on mature and young plants; calyx 1.5–2.0 cm long ..... 11. *B. hymenaeifolia*

1. **Bauhinia aculeata** L., Sp. Pl. 374. 1753, non Vell., 1825. TYPE: Colombia or Venezuela, *Herb. Clifford* (BM, holotype, not seen, IJ, photo).

B. emarginata Miller, Gard. Dict., ed. 8. 1768, non Jack, 1822, nec Wall., 1831, nec. Roxb. ex G. Don, 1832. TYPES: Colombia, Bolívar, Houston s.n. (BM, holotype, not seen, IJ, US, photos).
B. rotundata Miller, Gard. Dict., ed. 8. 1768. TYPE: Colombia, Bolívar, *Houston s.n.* (BM, holotype, not seen, US, photo).
B. ungula Jacq., Frag. Bot. 22. 1801, non Willd. ex Steud., 1840. TYPE: Venezuela, *Jacquin s.n.* (W, holotype, not seen).
Pauletia glandulosa H.B.K., Nov. Gen. Sp. Pl. 6: 314. 1824. TYPE: Venezuela, Sucre, *Humboldt 47* (P, holotype, not seen, MO microfiche; B(W), isotype, not seen, F, MO, NY, US, photos).
Bauhinia glandulosa (H.B.K.) DC., Prodr. 2: 513. 1825.

B. affinis Vogel, Linnaea 10: 594. 1836. TYPE: Brazil, Santa Catharina, *Vogel s.n.* (B, holotype, not seen, probably no longer extant, MO, NY, photos).
B. bredmeyeri Vogel, Linnaea 13: 302. 1839. TYPE: Venezuela, Distrito Federal, *Bredmeyer s.n.* (B, holotype, not seen, F, fragment, F, MO, NY, US, photos).
B. albicans Vogel, Linnaea 13: 304. 1839. TYPE: Brazil, Rio de Janeiro, *Sello 201* (B, holotype, not seen, F, fragment, MO, NY, US, photos).
B. ungula Willd. ex Steud., Nom. Bot., ed. 2. 1: 191. 1840, pro syn., non Jacq., 1801.
B. notophila Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 166. 1879. TYPE: not known.
B. catingae Harms, Bot. Jahrb. Syst. 42: 209. 1908. TYPE: Brazil, Bahia, *Ule 7277* (B, holotype, not seen, F, fragment, F, MO, NY, US, photos; K, isotype, not seen, F, NY, US, photos).
B. mollicella Blake, Contr. Gray Herb. 53: 32. 1918. TYPE: Venezuela, *Curran & Hamon 1024* (GH, holotype, not seen; NY, US, isotypes).
B. miranda Pittier, Trab. Mus. Comercial Venez. 1: 13. 1927. TYPE: Venezuela, Miranda, *Pittier 11783* (VEN, holotype, not seen; NY, US, isotypes).
B. mollifolia Pittier, Trab. Mus. Comercial Venez. 1: 14. 1927. TYPE: Venezuela, Cojedes, *Pittier 11726* (VEN, holotype, not seen; NY, US, isotypes).
B. schultzei Harms, Repert. Spec. Nov. Regni Veg. 24: 210. 1928. TYPE: Colombia, Magdalena, *Schultze 428* (B, holotype, not seen, F, fragment, F, MO, NY, US, photos).
B. albiflora Britton & Rose, N. Amer. Fl. 23: 203. 1930. TYPE: El Salvador, Sonsonate, *Standley 22373* (US, holotype; NY, isotype).
Pauletia affinis (Vogel) Schmitz, Bull. Jard. Bot. Natl. Belgique 43: 388. 1973.

This species was referred to *B. emarginata* Miller by Schery (1951). In Panama it is known only from the Province of Panamá. The Panamanian material belongs to var. *aculeata* which is also found in El Salvador, Antigua, Barbados, Peru, Brazil, Bolivia, and Argentina. A second variety, var. *grandiflora* (Juss.) Wunderlin, distinguished by its larger leaves, flowers, and fruits, occurs in Ecuador, Peru, Bolivia, and Argentina.

Bauhinia albiflora Britton & Rose, from El Salvador, is described as having five fertile stamens. However, examination of type material of this species revealed it to actually have ten stamens. Material from El Salvador referred to *B. albiflora* is indistinguishable in all respects from *B. aculeata.*

This taxon is highly variable as is evidenced by its extensive synonymy, and it is not surprising that Schery expressed uncertainty in selecting a name for the Panamanian material.

2. **Bauhinia pauletia** Pers., Syn. Pl. 1: 455. 1805. TYPE: Panama, Panamá, *Herb. Cavanilles* (MA, holotype, not seen).

Pauletia aculeata Cav., Icon. Descr. Pl. 5: 6. 1799. TYPE: Panama, Panamá, *Herb. Cavanilles* (MA, holotype, not seen).
Bauhinia spinosa Poir., Encycl. Méth. Bot. Suppl. 1: 599. 1811, new name for *Pauletia aculeata* Cav.
B. leptopetala DC., Prodr. 2: 513. 1825. TYPE: Based on a Sessé and Mocino plate known only from a copy at Geneva (G, not seen), photos (F, MO, US), tracing (US), and photos of tracing (MO, US).
B. panamensis Spreng., Syst. Veg. 2: 334. 1825, new name for *Pauletia aculeata* Cav.
B. parvifolia Seem., Bot. Voy. Herald 113. 1854, non Hochst. ex Field & Gard., 1844, nec Teijsm. & Binn., 1867. TYPE: Panama, Panamá, *Seemann 223* (K, holotype, not seen, F, NY, US, photos).
B. chlorantha Brandegee, Zoe 5: 200. 1905. TYPE: Mexico, Sinaloa, *Brandegee s.n.* (UC, holotype, not seen; US, isotype).
B. longiflora Rose, Contr. U.S. Natl. Herb. 10: 97. 1906, non (Bong.) Steud., 1840. TYPE: Mexico, Sinaloa, *Palmer 1426* (US, holotype; NY, US, isotypes).

This species is known in Panama from the Provinces of Herrera, Panamá, Los Santos, and the Canal Zone. It ranges from western Mexico south to Colombia and Venezuela. In the Caribbean it is found in Trinidad and has been introduced into Puerto Rico where it apparently has become naturalized.

Bauhinia pauletia is one of two Panamanian species known to be bat pollinated (Heithaus et al., 1974) with the other species being *B. ungulata.*

3. **Bauhinia picta** (H.B.K.) DC., Prodr. 2: 515. 1825.

Pauletia picta H.B.K., Nov. Gen. Sp. Pl. 6: 316. 1824. TYPE: Colombia, Santander, *Humboldt 1604* (P, holotype; B, isotype, probably no longer extant, F, MO, NY, US, photos).
Bauhinia ligulata Pittier, Contr. U.S. Natl. Herb. 20: 112. 1918. TYPE: Panama, San Blas, *Pittier 4334* (US, holotype; US, isotype).
B. kalbreyeri Harms, Repert. Spec. Nov. Regni Veg. 19: 65. 1923. TYPE: Colombia, Antiquia, *Kalbreyer 1802* (US, holotype; US, isotype).
B. conceptionis Britton & Killip, Ann. New York Acad. Sci. 35: 160. 1936. TYPE: Colombia, Chocó, *Archer 2086* (NY, holotype, not seen; US, isotype).

This species was first reported from Panama by Pittier who described material from Puerto Obaldía, San Blas, as a new species, *B. ligulata.* It is today still only known in Panama from the type material of *B. ligulata. Bauhinia picta* also occurs in Venezuela and Colombia where it is also occasionally cultivated as an ornamental.

Bauhinia picta is distinguished from all other Panamanian species of *Bauhinia* by its eight fertile stamens and the presence of two ligulate staminodes. Schery (1951) erroneously described this species as having ten fertile stamens.

4. **Bauhinia ungulata** L., Sp. Pl. 374. 1753. TYPE: *Herb. Miller* (BM, holotype, not seen).

Pauletia inermis Cav., Icon. Descr. Pl. 5: 6. 1799. TYPE: Mexico, Guerrero, *Herb. Cavanilles* (MA, holotype, not seen).
Bauhinia inermis (Cav.) Pers., Syn. Pl. 1: 455. 1805, non Forsk., 1775, nec. Billb. ex Walp., 1843.
Cansenia ungulata (L.) Raf., Sylva Tell. 122. 1838.
Bauhinia cavanillei Millsp., Publ. Field Columbian Mus. Bot. Ser. 1: 364. 1898, new name for *Pauletia inermis* Cav.
Pauletia ungulata (L.) Schmitz, Bull. Jard. Bot. Natl. Belgique 43: 393. 1973.

Numerous additional synonyms occur for this highly variable species based on South American material, but are excluded here for brevity.

Bauhinia ungulata is known in Panama from the Provinces of Chiriquí, Darién, Herrera, Veraguas, and the Canal Zone. It ranges from Mexico south to Paraguay. *Bauhinia ungulata* is known to be bat pollinated, as also is *B. pauletia* (Heithaus et al., 1974).

5. **Bauhinia beguinotii** Cufod., Arch. Bot. Sist. 9: 192. 1933. TYPE: Costa Rican, Limón, *Cufodontis 664* (W, holotype, not seen, F, MO, US, photos).

Shrubs or small *trees* to 6 m tall; branches brown-tomentose to -tomentellous when young, soon glabrescent. *Leaves* petiolate; blade oblong-ovate, entire or with bifurcate apices 10–24 cm long, 5–16 cm wide, the apices acuminate to

caudate, simple or bifurcate, the base rounded to truncate, chartaceous, glabrate above, brown-tomentellous below, 7–9-nerved; petiole 1.5–3.5 cm long, slightly canaliculate; stipules broadly ovate, apiculate, 1.0–1.5 mm long, persistent; intrastipular excrescences subulate, the adpetiolar pair occasionally enlarged up to 1 mm in length. *Inflorescences* racemose, terminal or subterminal and axillary, the racemes 5–10-flowered, the rachis brown-tomentose to -tomentellous, the buds elliptic-lanceolate, 1.5–2.5 cm long, brown-tomentose to -tomentellous, the free tips minute; bract ovate, ca. 1 mm long; bracteoles similar to the bract, subbasal; pedicels 2–5 mm long. *Flowers* with the hypanthium cyathiform, 5–6 mm long; calyx spathaceous at anthesis; petals 5, subequal, 2.5–4.5 cm, the blade white, oblanceolate to elliptic, 0.8–2.0 cm wide, glabrous, the claw 3–5 mm long, pale pink, glabrate; fertile stamens 10, the 5 alternate ones longer, ca. ¾ the length of petals, connate up to ca. ½ the length of shorter stamens, the filaments sparsely pilose toward base or glabrate, the anthers oblong in bud, triangular to lanceolate at anthesis, rounded to emarginate at the apex, sagittate at the base, 2–3 mm long, sparsely pilose or glabrate; gynoecium ± equalling the stamens, brown-tomentose or -tomentellous, the gynophore ± equalling the style, the stigma bilobate. *Fruits* dehiscent legumes, linear, apiculate with a persistent style, 12–15 cm long, ca. 2 cm wide, minutely strigose to glabrate, the gynophore 1.0–1.5 cm long, glabrate; seeds not seen.

A rare species previously known only from Limón Province, Costa Rica, and Gorgona Island, Narino Province, Colombia. It is reported here for the first time from Panama. The Colombian material, recognized as var. *gorgonae* (Killip ex Cowan) Wunderlin, is distinguished from the Costa Rican and Panamanian material in having its leaves deeply bilobate or bifoliolate rather than entirely or only slightly bilobed. Since the degree of lobing in leaves is a function of age of the plant in some species of *Bauhinia*, it is possible that when additional material is found, the two varieties may prove to be synonymous. In Panama the species is represented by a single collection.

PANAMA: El Lllano-Cartí-Tupile road, 16 km N of Pan-American Hwy. at El Llano, 400–500 m, *Nee 9362* (MO).

6. **Bauhinia petiolata** (Mutis ex DC.) Triana ex Hook. f., Bot. Mag. *tab. 6277.* 1877.

Amaria petiolata Mutis ex DC., Prodr. 2: 519. 1825. TYPE: Colombia, *Mutis 2398* (MA, holotype, not seen; US, isotype).
A. sessilifolia Mutis ex DC., Prodr. 2: 519. 1825. TYPE: Colombia, *Mutis 2724* (MA, holotype, not seen, US, fragment).
Casparia speciosa Linden ex Hook. f., Bot. Mag. *tab. 6277.* 1877, pro syn.
Bauhinia caudigera Blake, Contr. U.S. Natl. Herb. 20: 533. 1924. TYPE: Venezuela, Yaracuy or Carabobo, *Pittier 8851* (US, holotype, US, NY, photos; P, isotype).
Schnella caudigera (Blake) Pittier, Suppl. Pl. Usual. Venez. 37: 1939.

Shrubs or small *trees* to 8 m tall; branches slender, glabrous. *Leaves* petiolate; blade ovate to ovate-lanceolate, entire, 7–14 cm long, 3–7 cm wide, the apices caudate, the base rounded to truncate, chartaceous, glabrous above, obscurely strigillose along the veins or glabrate below, 5-nerved; petiole 1–3 cm long, slightly canaliculate; stipules ovate to reniform, ca. 1 mm long, persistent and

becoming calloused, intrastipular excrescenses obscure. *Inflorescences* shortly racemose, terminal or subterminal and axillary, the racemes 3–8-flowered, the rachis tomentellous or glabrate, the buds narrowly ellipsoid, ca. 4 cm long, tomentellous to glabrate; bract broadly ovate, ca. 1 mm long, ciliolate; bracteoles similar to the bract, subbasal; pedicels ca. 4–7 mm long. *Flowers* with the hypanthium campanulate, 5–10 mm long; calyx spathaceous at anthesis; petals 5, subequal, 3–5 mm long, white, the blade oblanceolate, 1.0–1.5 cm wide, glabrous, the claw 2–5 mm long, glabrous; fertile stamens 10, slightly shorter than petals, the alternate ones slightly shorter, slightly connate at the base, glabrate, the anthers linear, 7–10 mm long, sparsely pilose or glabrate, sagittate at the base; gynoecium slightly exceeding the petals, glabrate, the gynophore ± equalling the style or slightly shorter, the stigma bilobate. *Fruits* dehiscent legumes, linear, apiculate with a persistent style, 20–30 cm long, 2–3 cm wide, glabrous, the gynaphore ca. 2 cm long; mature seeds not seen.

A rare species previously known only from Colombia and Venezuela. It is here reported from Panama for the first time.

COLÓN: Ca. 2–3 mi up the Río Guanche, ca. 10–20 m, *Kennedy & Foster 2127* (MO, USF).

7. **Bauhinia microstachya** (Raddi) Macbride, Contr. Gray Herb. 59: 22. 1919.

Schnella microstachya Raddi, Mem. Soc. Ital. Modena 18: 412. 1820. TYPE: not known.
Bauhinia gentlei Lundell, Wrightia 3: 120. 1965. TYPE: Belize, Toledo, *Gentle 6047* [TEX(LL), holotype, not seen].

Numerous additional synonyms occur for this species based on South American material, but are excluded here for brevity.

Tendrilled *vines*; branches slender, brown-sericeous or -tomentose when young, soon glabrescent, the older stems sinuate-flattened; intrastipular tendrils 1 or paired, woody, circinate. *Leaves* broadly ovate, bilobate to ½ their length, 3–9 cm long, 3–9 cm wide, the lobes rounded to acute, the base cordate to truncate, chartaceous, glabrate above, pilose-tomentose or sparsely appressed pilose below, especially along the nerves, 7–9-nerved; petiole 2–4 cm long; stipules lanceolate, ca. 1 mm long, caducous. *Inflorescences* racemose or subpaniculate, terminal or subterminal and axillary, 5–25 cm long, brown-sericeous or -tomentose, many-flowered, the buds ovoid, ca. 5 mm long; bract linear to lanceolate, ca. 0.5 mm long, caducous; bracteoles similar to the bract, above the middle of the pedicel; pedicels subsessile to 5 mm long. *Flowers* with the hypanthium discoid, ca. 0.5 mm high; calyx campanulate, 5-lobed, the lobes ca. ½ the length of the calyx; petals 5, 5–7 mm long, the blade elliptic to spatulate, sparsely pilose externally or glabrous, the claw to ½ the length of the blade; fertile stamens 10, free, nearly equalling the petals, the alternate ones slightly shorter, the filaments slender, glabrous, the anthers oblong, 1.5–2.0 mm long, glabrous; gynoecium ± equalling the petals, subsessile, the ovary sericeous, the style glabrate, acentric, shorter than the ovary, the stigma terminal, capitate. *Fruits* indehiscent legumes, oblong, chartaceous-walled, mucronate with a persistent style, ca. 5 cm long, ca. 1.5 cm wide; seeds 1–3, suborbicular, ca. 1 cm in diameter.

A widespread, but uncommon, South American species with a disjunction in Guatemala and Belize, it is reported here for the first time from Panama.

DARIÉN: Cerro Yaviza, *Duke & Bristan 422* (MO, NY, US). Río Tuira, between Río Punusa and Río Mangle, *Duke 14582* (MO). La Boca de Pirre, *Bristan 1296* (MO, NY). Sambú, 0–5 mi above Río Venado, *Duke 9285* (MO, NY, US).

8. **Bauhinia glabra** Jacq., Enum. Pl. Carib. 20. 1760. TYPE: not seen.

B. heterophylla Kunth, Voy. Reg. Equin., Bot., Mim. 157. 1824. TYPE: Venezuela, Carabora, *Humboldt 1187* (P, lectotype; B(W), isolectotype, not seen, F, MO, NY, US, photos).
B. suaveolens H.B.K., Nov. Gen. Sp. Pl. 6: 320. 1824. TYPE: Peru, San Martín, *Humboldt 3588* (P, lectotype; B(W), isolectotype, not seen, F, MO, NY, US, photos).
B. cumanensis H.B.K., Nov. Gen. Sp. Pl. 321. 1824. TYPE: not seen.
B. columbiensis Vogel, Linnaea 13: 313. 1839. TYPE: not seen.
Binaria cumanensis (H.B.K.) Raf., Sylva Tell. 122. 1838.
Schnella brachystachya Benth., J. Bot. (Hooker) 2: 98. 1840. TYPE: Guyana, Essequibo, *Schomburgk 565* (K, holotype, not seen, NY, US, photos; F, P, US, isotypes).
Bauhinia brachystachya (Benth.) Walp., Repert. Bot. Syst. 1: 852. 1843.
Schnella columbiensis (Vogel) Benth., Bot. voy. Sulph. 89. 1844.
S. heterophylla (Kunth) Benth. in Griseb., Cat. Pl. Cub. 81. 1866.
Caulotretus heterophyllus (H.B.K.) Warb., Bot. Zeitung (Berlin) 41: 617. 1883.
Bauhinia standleyi Rose, J. Wash. Acad. Sci. 17: 166. 1927. TYPE: Panama, Panamá, *Standley 2647* (US, holotype, NY, fragment; NY, isotype).
Schnella cummanensis (H.B.K.) Britton & Rose, N. Amer. Fl. 23: 206. 1930.
S. standleyi (Rose) Britton & Rose, N. Amer. Fl. 23: 206. 1930.
S. storkii Rose in Britton & Rose, N. Amer. Fl. 23: 206. 1930. TYPE: Panama, Bocas del Toro, *Stork 140* (US, holotype, NY, fragment; UC, isotype).
Bauhinia hondurensis Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 313. 1931. TYPE: Honduras, Atlantida, *Chickering 152* (F, holotype).
B. storkii (Rose) Standley, Trop. Woods 34: 40. 1933.
Schnella glabra (Jacq.) Dugand, Revista Acad. Colomb. Ci. Exact. 4: 137. 194.
Binaria hondurensis (Standley) Schmitz, Bull. Jard. Bot. Natl. Belgique 43: 403. 1973.

Numerous additional synonyms occur for this highly variable species based on South American material. Only the names used for Panamanian or Central American material are included here for brevity.

Schery (1951) referred this species in part to *B. standleyi*, *B. storkii*, and *B. cumanensis*. However, he did indicate that *B. standleyi* and *B. cumanensis* might both be synonymous with *B. glabra*. *Bauhinia storkii* is actually little more than a pinkish-flowered, hirsute form.

In addition, *B. suaveolens*, excluded by Schery as a species of doubtful occurrence in Panama, is also placed in synonymy with *B. glabra*.

Bauhinia glabra is a widespread species ranging from the state of Chiapas in Mexico south and throughout most of the northern half of South America. It also occurs in Cuba and Trinidad in the Caribbean. In Panama it is known from the Provinces of Bocas del Toro, Coclé, Darién, Los Santos, Panamá, and the Canal Zone.

Bauhinia glabra is highly variable in leaf size, shape, and vesture. Certain combinations of leaf morphology and vesture are more frequent in some geographic areas, but intergradations are common. These various forms therefore do not warrant taxonomic recognition and are best considered, at best, only as biotypes. Numerous taxa have been described on the basis of these variable characters resulting in a lengthy synonymy for the species.

9. **Bauhinia reflexa** Schery, Ann. Missouri Bot. Gard. 38: 17. 1951. TYPE: Panama, Canal Zone, *Woodson et al. 1623* (MO, holotype; NY, US, isotypes).

A distinctive species described by and known only to Schery from collections made in the Canal Zone. It is now known from the Provinces of Darién, Panamá, and San Blas, as well as the Provinces of Valle and Chocó of Colombia.

10. **Bauhinia guianensis** Aubl., Hist. Pl. Guiane 1: 377. 1775. TYPE: French Guiana; *Aublet s.n.* (? BM, holotype, not seen).

B. splendens H.B.K., Nov. Gen. Sp. Pl. 6: 321. 1824. TYPE: ? Venezuela, *Humboldt 1186* [B(W), holotype, not seen, F, MO, US, photos].
Schnella excisa Griseb., Fl. Brit. W. Ind. 214. 1860. TYPE: Trinidad, *Crueger 57* (K, holotype, not seen, IJ, photo).
Bauhinia excisa (Griseb.) Hemsley, Biol. Centr. Amer., Bot. 1: 377. 1880.
B. obovata Blake, J. Wash. Acad. Sci. 14: 286. 1924. TYPE: Panama, Darién, *Pittier 5568* (US, holotype; F, NY, US, isotypes).
Schnella obovata (Blake) Britton & Rose, N. Amer. Fl. 23: 207. 1930.
Bauhinia sericella Standley, Publ. Carnegie Inst. Wash. 461: 60. 1935. TYPE: Belize, Toledo, *Schipp 1197* (F, holotype; F, MO, NY, UC, isotypes).
B. manca Standley Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 511. 1937. TYPE: Costa Rica, Alajuela, *Brenes 20552* (F, holotype; NY, isotype).
B. thompsonii I. M. Johnston, Sargentia 8: 140. 1949. TYPE: Panama, Panamá, *Johnston 539* (A, holotype; NY, US, isotypes).

A highly variable and widespread species with an almost unbelievably large and complex synonymy based essentially on South American material. Only the names which have been used for Panamanian and Central American material are included here for brevity. In addition, *B. platycalyx* Benth., *B. breviloba* Ducke, and *B. umbriana* Britton & Killip, incidently mentioned by Schery (1951), should also be sought here.

Schery referred this species in part to *B. obovata*, *B. excisa*, and *B. manca*, which illustrate its variable nature.

Bauhinia guianensis is a widespread species ranging from southern Mexico south and throughout most of the northern half of South America. It is also found on Trinidad in the Caribbean. In Panama it is found in the Provinces of Coclé, Colón, Darién, Panamá, San Blas, Veraguas, and the Canal Zone. It was reported by Schery from Bocas del Toro based on *Dunlap 337* from Changuinola Valley, but this collection is correctly assigned to *B. glabra*.

Bauhinia guianensis is highly variable in leaf size, shape, and vesture. Immature specimens usually have leaves bifoliolate or at least deeply bilobate while older, more mature specimens usually have shallowly bilobate (less commonly entire) leaves. However, it is not unusual to find a wide range of leaf shapes and sizes on the same individual. Certain combination of leaf morphology and vesture types are often more common in some geographical areas, but intergradations are also common. Thus these forms do not warrant taxonomic recognition and are considered, at best, biotypes. Numerous species and infraspecific taxa have been described on the basis of these variable vegetative characters, resulting in a lengthy synonymy for the species.

11. **Bauhinia hymenaeifolia** Triana ex Hemsley, Diag. Pl. Nov. 48. 1880. TYPE: Panama, Canal Zone, *Hayes 635* (K, holotype, not seen, US, photo; P, isotype, US, photo).

B. eucosma Blake, J. Wash. Acad. Sci. 14: 286. 1924. TYPE: Panama, Canal Zone, *Pittier 6782* (US, holotype, NY, fragment; P, US, isotypes).
Schnella eucosma (Blake) Britton & Rose, N. Amer. Fl. 23: 207. 1930.
S. *hymenaeifolia* (Triana ex Hemsley) Britton & Rose, N. Amer. Fl. 23: 208. 1930.
Binaria hymenaeifolia (Triana ex Hemsley) Schmitz, Bull. Jard. Bot. Natl. Belgique 43: 404. 1973.

Hemsley erroneously stated that *B. hymenaoifolia* has five fertile stamens, but examination of the type material revealed it has ten. Schery (1951) accordingly distinguished it from *B. eucosma* on the basis of Hemsley's statement of stamen number and referred nearly all of the Panamanian material to *B. eucosma.*

The Panamanian material is referred to var. *hymenaeifolia* and is distinguished from the Colombian material which is referred to var. *stuebeliana,* (Harms) Wunderlin. Variety *hymenaeifolia* has chartaceous leaves and white flowers while var. *stuebeliana* has subcoriaceous leaves and pink flowers.

Bauhinia hymenaeifolia is known in Panama only from the Provinces of Panamá, Darién, and the Canal Zone.

LITERATURE CITED

HEITHAUS, E. R., P. A. OPLER & H. G. BAKER. 1974. Bat activity and pollination of *Bauhinia pauletia*: plant-pollinator coevolution. Ecology 55: 412–419.
SCHERY, R. W. 1951. Leguminosae, subfamily Caesalpinoideae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 38: 1–94.
WUNDERLIN, R. P. 1975. Enumeration and typification of genera in the tribe Cercеae (Leguminosae). Rhodora 77: (in press).

UNION OF *CHIONANTHUS* AND *LINOCIERA* (OLEACEAE)

WILLIAM T. STEARN[1]

ABSTRACT

Reasons for the union of *Chionanthus* and *Linociera* are presented, and the following new combinations are made: *Chionanthus guianensis* (Aublet) Stearn, *C. panamensis* (Standley) Stearn, *C. bakeri* (Urban) Stearn, *C. axilliflorus* (Griseb.) Stearn, *C. cubensis* (P. Wilson) Stearn, *C. bumelioides* (Griseb.) Stearn, *C. dictyophyllus* (Urban) Stearn, *C. urbanii* (Knobl.) Stearn, *C. dussii* (Krug & Urban) Stearn, and *C. holdridgii* (Camp & Monachino) Stearn.

A survey of morphological together with palynological characters in a diversity of species from America, Africa and Asia, which have been referred to the genera *Chionanthus* L., *Mayepea* Aublet, *Linociera* Swartz and *Tessarandra* Miers, a survey undertaken in the hope of finding correlated diagnostic characters which would permit at least the maintenance of *Chionanthus* and *Linociera* as distinct genera in volume 6 (ined.) of the *Flora of Jamaica*, has convinced me that these must all be treated as congeneric. The correct name for this large essentially tropical group commonly known as *Linociera* is *Chionanthus*, based on one of its few temperate representatives, the North American *Chionanthus virginicus* L.

This shrub or small tree loses its leaves in autumn and covers itself in spring with drooping panicles of white flowers, easily recognizable by their four linear corolla lobes and two short stamens. It had reached Dutch gardens by 1736 and was already known there as "Sneebaum" or "Sneeuwboom" (snow tree), a vernacular name which led Linnaeus's friend Adrian van Royen to suggest the generic name *Chionanthus* (from χιων, chiōn, snow). Linnaeus adopted this in the first edition (1737) as well as the fifth edition (1754) of his *Genera Plantarum* and used it in his *Hortus Cliffortianus* (1738). He named the species *Chionanthus virginica* in the *Species Plantarum* (1753), treating the generic name as feminine because the plants were trees or large shrubs. It is the lectotype of *Chionanthus*, Linnaeus having added in 1747 a Ceylon species, his *C. zeylonica*, with which *Thouinia nutans* L. f. (1781) and *Chionanthus purpureus* Lam. (*Linociera purpurea* (Lam.) Vahl) are conspecific.

In 1775 Aublet published the name *Mayepea guianensis* in his *Histoire des Plantes de la Guiane Françoise* (Vol. 1: 81, *tab. 31*) for a plant found in French Guiana, the generic name being a latinization of a vernacular name "Mayepé." No known plant, however, exactly corresponds to Aublet's illustration. Some apparently alternate leaves are possibly due to one leaf of a pair falling before the other. The attribution of four stamens may be due to an error of observation influenced by the existence of four corolla lobes or, since *Chionanthus virginicus*, though normally with two stamens in a flower, sometimes produces four, Aublet may have chanced upon an abnormal specimen. The Aublet specimen representative of his *Mayepea guianensis* in the general herbarium of the British

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Museum (Natural History) has only two stamens, as Banks's botanist librarian Daniel Solander (1736–1782) noted long ago. The anthers of this specimen are essentially as figured by Aublet; each rests in the concave base of a corolla lobe and is oblong with a rounded apex, the connective not being continued upwards as in the West Indian species commonly known as *Linociera compacta*. It represents a species probably confined to Guiana, **Chionanthus guianensis** (Aublet) Stearn, and is distinct from *C. compactus* Swartz.

In 1788 Swartz gave the name *Thouinia ligustrina* in his *Nova Genera et Species* to a small evergreen Jamaican tree which has corolla lobes only 5–7 mm long and stamens more or less equalling them. The name *Thouinia* commemorated the French gardener André Thouin (1747–1824), to whom, however, the younger Linnaeus had dedicated in 1781 another *Thouinia* based on a Ceylon species, his father's *Chionanthus zeylonicus*. Swartz accordingly proposed the new name *Linociera* for his own genus in a letter to Schreber, and it accordingly appeared as *Linociera* in Schreber's *Genera Plantarum* (1791). This commemorated a 16th century French physician, Geoffrey Linocier of Tours. The type remains *Thouinia ligustina* Swartz, i.e., *Chionanthus ligustrinus* (Swartz) Persoon.

Since then a large number of species from the West Indies, Middle America, northern South America, tropical Africa, Asia, and Australia have been added to *Linociera*, their inclusion so increasing the range of morphological characters within the group that as long ago as 1860 Thwaites wrote "as remarked by Blume, there seems scarcely sufficient ground for separating *Linociera* as a genus from *Chionanthus*."

Johnston (1957) in a review of the family Oleaceae distinguished them as well as it seems possible to do so:

Linociera. Foliage usually evergreen; leaves ± coriaceous, except in young shoots (rarely deciduous and rather thin). Corolla lobes slightly to considerably elongated (but less than 1.0 cm long), united in a short tube or in pairs at the base or quite free. Inflorescence an axillary panicle, sometimes condensed and fasciclelike or reduced and racemose; pedicels various but less than 0.6 cm long. Tropics and subtropics of Africa, Asia, Malaysia, Australia and America.

Chionanthus. Foliage deciduous; leaves thin-textured. Corolla lobes much elongated (1.5–4 cm) and linear, united at base only. Inflorescence a terminal or axillary panicle; pedicels slender 0.6–1.5 cm long. Eastern Asia and Eastern North America.

As is indeed evident from Johnston's failure to find any clear-cut nonoverlapping characters for their distinction, the two merge completely; it has simply been a convention to refer temperate species to *Chionanthus* and tropical ones to *Linociera*. Thus the deciduous Ecuador species *Chionanthus pubescens* Kunth [*Linociera pubescens* (Kunth) Eichler], produces its inflorescences on leafless shoots like *Chionanthus virginicus*. *Chionanthus pygmaeus* Small, a deciduous Florida species, has corolla lobes about 1 cm long like various evergreen tropical species of *Linociera*. **Chionanthus panamensis** (Standley) Stearn (*Linociera panamensis* Standley, Publ. Field Columbian Mus., Bot. Ser.

8: 32. 1930.) on the other hand has corolla lobes to 2 cm long. Greater differences exist between various tropical species referred to *Linociera* than between the types of *Chionanthus* and *Linociera*. Palynological characters likewise fail to provide other than specific differences.

This survey began unambitiously with establishing the correct nomenclature for species of the group occurring in Jamaica. These are *Chionanthus domingensis* Lam., *C. ligustrinus* (Swartz) Persoon, ***C. jamaicensis*** (Urban) Stearn (*Linociera jamaicensis* Urban, Symb. Antill. 2: 456. 1901.) and new species awaiting publication in a general synopsis of tropical American species; this grew from that of the Jamaican and Cayman Island species. The nomenclature of the Cuban species, to which Alain provides a key under the name *Linociera* in León & Alain (1957) becomes as follows: *Chionanthus ligustrinus* (Swartz) Persoon, *C. domingensis* Lam., **C. bakeri** (Urban) Stearn (*Linociera bakeri* Urban, Symb. Antill. 5: 530. 1908.), **C. axilliflorus** (Griseb.) Stearn (*Linociera axilliflora* Griseb., Mem. Amer. Acad. Arts, n.s., 8: 519. 1862.), **C. cubensis** (P. Wilson) Stearn (*Mayepea cubensis* P. Wilson, Bull. Torrey Bot. Club. 42: 390. 1915.) and **C. bumelioides** (Griseb.) Stearn (*Linociera bumelioides* Griseb., Cat. Pl. Cuba 169. 1866.). Other West Indian species are **Chionanthus dictyophyllus** (Urban) Stearn (*Linociera dictyophylla* Urban, Ark. Bot. 22A (no. 8): 88. 1929.) from Haiti, **C. urbanii** (Knobl.) Stearn (*Linociera urbanii* Knobl., Repert. Spec. Nov. Regni Veg. 33: 178. 1933.) from Haiti, **C. dussii** (Krug & Urban) Stearn (*Mayepea dussii* Krug & Urban, Bot. Jahrb. Syst. 15: 347. 1892.) from Martinique, and **C. holdridgii** (Camp & Monachino) Stearn (*Linociera holdridgii* Camp & Monachino, Lloydia 2: 223. 1939.) from Puerto Rico.

Literature Cited

Johnston, L. A. S. 1957. A review of the family Oleaceae. Contr. New South Wales Natl. Herb. 2: 395–418.

León, H. & H. Alain. 1957. Flora de Cuba. Vol. 4. Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle" 10: 1–556.

NOTES ON CENTRAL AND SOUTH AMERICAN *CISSUS* (VITACEAE)[1]

THOMAS B. CROAT[2]

ABSTRACT

Cissus allenii Croat and *Cissus neei* Croat are described as new. *Cissus allenii* differs from *C. microcarpa* Vahl, to which it may be most closely related, in being puberulent whereas *C. microcarpa* has a combination of crisped-villous and appressed T-shaped pubescence. *Cissus neei* is distinguished from other unifoliolate species in Panama by its thick glabrous leaves, greenish flowers, and glabrous inflorescence. It is perhaps most closely related to *Cissus brevipes* Morton & Standley, but that species differs in having thinner, conspicuously toothed leaves. The following new distributional reports are made: *Cissus brevipes* in Panama, *C. ulmifolia* (Baker) *Planchon* in Ecuador and Panama, *C. martiniana* Woodson & Seibert in Mexico, *C. biformifolia* Standley in Colombia, and *C. pseudosicyoides* Croat in Ecuador.

Since the Vitaceae was completed for the *Flora of Panama* (Elias, 1968), several species have been found to be new to the flora. One of these was the subject of an earlier report (Croat, 1973). This report concerns four additional species new to Panama, two being newly described. Thus five additional species have been collected in Panama since the treatment for the Vitaceae was completed.

Cissus allenii Croat, sp. nov.

Frutex scandens; folius trifoliolatus; lamina ovata-elliptica, 7–11 cm longa, 2.5–5.5 cm lata. Flores pallide virelli, circa 2 mm longi. Fructus immaturi, obovati, circa 4 mm longi, lenticellis.

Slender *lianas*; stems puberulous when young, weakly viscidulous, glabrescent, terete, becoming sparsely lenticellulate. *Leaves* trifoliolate; leaflets gradually acuminate at the apex, sharply serrate throughout most of their length, the upper surface glabrous except hirtellous on the midrib, the lower surface hirtellous on the principal veins; terminal leaflet oblong-elliptic, obtuse to acute at the base, 7.5–12 cm long, 3.5–5.0 cm wide, the major lateral veins 6–8 pairs, gradually arcuate to the margin, the reticulate venation obscure; lateral leaflets similar except slightly shorter, inequilateral at the base, acute on the inner margin, obtuse or rounded on the outer margin, their petiolules 4–8 mm long. *Inflorescences* ca. 15 cm long, the branches and pedicels puberulent; pedicels ca. 3 mm long. *Flowers* with the calyces bowl shaped, 2.0–2.5 mm wide, glandular; petals narrowly deltoid, 1.5 mm wide, glabrous. *Fruits* obovoid, ca. 4 mm long (immature), conspicuously lenticellulate.

TYPE: PANAMA. PROVINCE OF COCLÉ: Foothills of Cerro Pilón near El Valle, ca. 900 m, *Duke & Correa 14714* (MO-1910853, holotype).

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Other collections seen: COSTA RICA. PUNTARENAS PROVINCE: Road to Golfito Dairy Pastures, fruits, 11 Nov. 1952, *Allen 6625* (US).

Cissus allenii is apparently not closely related to other Central American species in the genus but may be confused with *Cissus microcarpa* Vahl. That species differs from *C. allenii* in having thinner, more pubescent leaves with a mixture of crisped-villous trichomes and flattened T-shaped trichomes on the lower veins of the leaflets and also on the branches of the inflorescence and pedicels. In contrast *Cissus allenii* is sparsely puberulent on the lower veins and on the inflorescence parts.

The species flowers and fruits in the late rainy season. Immature fruits are known from October and November.

The species is known from Costa Rica and Panama. It is named in honor of Paul Allen who made the first collection.

Cissus neei Croat, sp. nov.—FIG. 1.

Frutex scandens, glaber; caules foliaque succulenta. Folius sessile aut petiolo ad 2 cm longo; lamina oblonga-elliptica, 4–14 cm longa, 1.5–6 cm lata. Pedunculi 1–2 cm longi; flores virelli, circa 3 mm longi; petala ad 2.2 mm longa. Fructus purpureus, circa 1.1 cm latus.

Herbaceous or suffrutescent *vines*, essentially glabrous throughout; older stems with many dark, round lenticels; at least the younger leaves, stems and inflorescence parts usually drying black. *Leaves* thick, somewhat fleshy, drying stiff, subcoriaceous, sessile or with petioles narrowly canaliculate, to 1.5 (rarely to 2) cm long; blades oblong-elliptic, abruptly acuminate at the apex, acute to obtuse at the base, 4–14 cm long, 1.5–6 cm wide, pinnately veined, entire, thick and ± succulent when fresh, drying subcoriaceous, the lowermost pair of veins continuing up along the margin to as much as the lower third of the blade, the remaining 3–5 principal pairs of lateral veins arcuate-ascending, weakly sunken on the upper surface. *Inflorescences* of umbelliform, leaf-opposed cymes, to ca. 4 cm diam.; peduncles 1–2 cm long, the secondary peduncles 3–10 mm long; pedicels ca. 2 mm long, braceteolate at base; bracts deltoid, weakly ciliolate on the margins. *Flowers* greenish, ca. 3 mm long; calyx cup shaped in bud, more broadly flared at anthesis, entire or weakly and bluntly 4-lobed; petals narrowly ovate, acute at the apex, cucullate within, ca. 2.2 mm long; stamens 4, to 1.2 mm long, the filaments glabrous, the anthers oblong, ca. 0.5 mm long; disc 4-lobed, saucer shaped; style 4-sided, reaching the lower edge of the anthers. *Fruits* globose, purple, to 1.1 cm diam.

TYPE: PANAMA. PROVINCE OF PANAMÁ: El Llano-Cartí Road, 12 km from PanAmerican Highway, vicinity of Gorgas Laboratory Mosquito Control Project #1, 360–400 m, flowers, 18 July 1974, *Croat 25084*. (MO-2276841, holotype; COL, F, K, NY, PMA, S, US, VEN, isotypes).

Other collections seen: PANAMA, PROVINCE OF PANAMÁ: El Llano-Cartí Road, vic. of Gorgas Laboratory Mosquito Control Project site at km 12, *Croat 26042* (MO); at 5 km, ca. 300 m, *Nee 7923* (MO, PMA, US); at 18 km, *Mori et al. 4585* (F, MO, PMA, TEX); at km 11–12, *Mori et al. 6895* (CAS, MO, NY, PMA, VEN).

FIGURES 1–2. *Cissus neei* Croat.—1. Habit (×1/20).—2. Close-up of leaves and flowers (×1/5).

The species is known only from premontane wet forest on the El Llano-Cartí Road. It is probably more widespread in Panama and should be expected to be found especially on the wetter Caribbean slope and in Darién Province.

Flowering is known from June to August. Fruits are known from November but fruits probably mature from September to November.

A second species of *Cissus* new to Panama and North America is *C. ulmifolia* (Baker) Planchon, known previously from Peru. The species was collected by Mori and Kallunki (*1857*) on the El Llano-Cartí Road, 9.6 km from the Pan-American Highway. The species was also recently collected in Ecuador by Gentry (*12490*) in the Department of Napo, 9–11 km S of Coca on the road to the Auca oil field. This is the first collection of the species from Ecuador known to me.

Of less interest is a report for *Cissus martiniana* Woodson & Seibert for Mexico. The species was collected in 1913 by Purpus (*7462*) in Chiapas at Cerro del Boquerón and more recently in Chiapas by Breedlove (*7462*) from the northwest slope of Zontehuitz in the Municipio of San Cristóbal de las Casas. The earlier collection was apparently overlooked in the *Flora of Panama* treatment as its range was reported as Guatemala to Panama.

Cissus biformifolia Standley is here reported for the first time for Colombia. The species was collected in Poponte, in the Magdalena River by Cyril Allen (*797*) in 1924, but the collection has previously been undetermined.

A third species of *Cissus* new to Panama is *C. brevipes* Morton & Standley collected recently by Gentry (*6899*) on the hills above El Valle in Coclé Province at ca. 1000 m. It was previously known only from Costa Rica. *Allen 182*, collected near El Valle in 1940 and despite bearing the name *C. brevipes*, was included under *C. sicyoides* in the *Flora of Panama* treatment.

Cissus pseudosicyoides Croat known previously to range from Costa Rica to Colombia is now also known from Ecuador based on *Gentry 12549*. The collection was made in the Department of Napo near the turn-off from the Coca-Los Aucas Road at km 4 at 250 m.

In order to facilitate identification of Panamanian material of *Cissus* a new key for Panama is presented here.

Key to *Cissus* in Panama

a. Leaves 3-foliolate.
  b. Stems 4-sided and prominently winged.
    c. Fruits ca. 3 cm diam.; petioles usually more than 7 cm long ..... *C. ulmifolia* (Baker) Planchon
    cc. Fruits less than 1 cm diam.; petioles less than 6 cm long ..... *C. erosa* L. Rich.
  bb. Stems terete or nearly so, not prominently winged.
    d. Mature peduncles (6–)7–12 cm long; stems 4-sided, often winged; fruits 4–6 mm diam. ..... *C. erosa* L. Rich.
    dd. Mature peduncles 1–3 cm long; stems terete to subangulate, wingless; fruits 6–10 mm diam. (mature fruits not seen for *C. allenii*).
      e. Terminal leaflets with a petiole 0.5–2.0 cm long; leaves mucronate-serrate, mature leaves 4–10 cm long.
        f. Pedicels appressed-pubescent with flattened T-shaped trichomes; pubescence of veins of lower leaflet surfaces (when present) of

crisped-villous trichomes and/or appressed T-shaped trichomes ..... *C. microcarpa* Vahl

ff. Pedicles puberulent; veins of the lower leaflet surface puberulent ..... *C. allenii* Croat

ee. Terminal leaflets sessile; leaves sparsely denticulate, mature leaves 2–4 cm long; flowers pale green; fruits ca. 1 cm diam. .. *C. martiniana* Woods.

aa. Leaves simple.

g. Pedicels glabrous; leaf blades monomorphic, the larger leaves at most rounded or truncate at the base, glabrous or villous, lacking T-shaped or puberulent trichomes.

h. Blades thin, often pubescent, ± ovate, rounded to truncate and with 2 or 3 pairs of lateral veins arising at or near the base, the margin serrate ..... *C. sicyoides* L.

hh. Blades thick, glabrous, oblong-elliptic, acute and with 1 pair of lateral veins at the base, the margin entire ..... *C. neei* Croat

gg. Pedicels definitely pubescent; leaf blades often dimorphic, the larger blades ovate-cordate, frequently with puberulent T-shaped trichomes.

i. Flowers red, the buds mostly 3–4 mm long; fruits 8–10 mm wide ..... *C. biformifolia* Standley

ii. Flowers greenish, cream or white, the buds mostly 1.5–2 mm long; fruits to 6 mm wide.

j. Petioles more than half as long as the blade; pedicels in part puberulent with stiff, erect, short trichomes ..... *C. pseudosicyoides* Croat

jj. Petioles less than ¼ as long as the blade; pedicels with flattened T-shaped trichomes, never puberulent as above ..... *C. brevipes* Morton & Standley

LITERATURE CITED

CROAT, T. B. 1973. A new species of *Cissus* (Vitaceae) for Central and South America. Ann. Missouri Bot. Gard. 60: 564–567.

ELIAS, T. S. 1968. Vitaceae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 55: 81–92.

NEW NAMES AND TAXA IN THE SOLANACEAE[1]

W. G. D'Arcy[2]

Abstract

Nicotiana cutleri D'Arcy, belonging to subgen. *Rustica*, sect. *Paniculatae*, *Witheringia exiguiflora* D'Arcy, and *W. morii* D'Arcy are newly described. Two new transfers are made: *Jaltoma viscosa* (Schrad.) D'Arcy & Davis from *Saracha*, and *Lycianthes sanctaeclarae* (Greenman) D'Arcy from *Solanum*. *Solanum stramoniifolium* is newly recorded for Panama.

Jaltomata viscosa (Schrad.) D'Arcy & Davis[3], comb. nov.

Saracha viscosa Schrad., Ind. Sem. Götting. 1832: 5. 1832, non Link ex D. Don, 1838. TYPE: Cult., Hort. Goettingen, *Schrader* (MO), seed received by Schrader from Spangenberg from Mexico.

Athenaea viscosa (Schrad.) Fernald, Proc. Amer. Acad. Arts 35: 567. 1900.

A. macrocardia Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 375. 1940. TYPE: Guatemala, below Finca Alejandria, Sierra de las Minas, Zacapa, *Steyermark 30004* (F, not seen, see Gentry & Standley, Fieldiana, Bot. 24 (10, 1 & 2): 7. 1974.

Herbs to 1 m tall, branching, the stems subterete, in part mottled purplish; viscose, pilose, the hairs erect, to 2 mm long, gland-tipped, dendritic, the branching distal on the hair, the gland golden, glistening, each gland secreting a golden globule of sticky fluid. *Leaves* geminate ovate, textilous, viscid, concolorous, entire or with 1–3 short deltoid-acuminate lobes, apically acuminate, basally truncate, the auricles crinkled, the veins 4–5 on each side, the basal 5 subdigitate, not anastomosing to form a distinct marginal vein, the minor venation somewhat impressed above, elevated beneath, pilose and conspicuous, evenly pubescent above with erect, mainly simple, gland-tipped hairs, beneath with shorter hairs except on the veins; petiole subterete but flattened on top, viscid-pilose, to 10 cm long, ca. 3 mm across basally, narrowing somewhat upwards. *Inflorescences* fasciculate in the axils of a pair of unequal leaves, to 10-flowered; pedicels terete, pilose, to 4 cm long, slender, expanded slightly near the apex, often recurved downwards. *Flowers* not showy, not fragrant; calyx 5-lobed about halfway down, the cup strongly angled, the angles rounded, saccate, ca. 1.5 cm across, slightly recessed at the point of pedicel insertion, viscid-pilose with simple hairs, the lobes unequal, cuneate, 1.5 cm long, pilose outside, inside with reduced, glandular hairs, slightly accrescent and turning red in fruit; corolla recurved-rotate, ca. 4 cm across, lobed halfway down, with 5 deltoid lobes, white with dark green mottling near the base of each lobe and proximal to it, drying bright yellow, the throat tomentose with white, eglandular, dendritic hairs, the ventral surface glabrous, the margins ciliate with white, mostly eglandular, submoniliform hairs, dorsally glabrous; stamens inserted near the top of the corolla tube, glabrous except for a few hairs near the base, white, slightly geniculate, ca. 10 mm long, somewhat unequal, the anthers ellipsoidal, purple, ca. 4 mm long, turning blue

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following anthesis; ovary ellipsoidal, glabrous, 4 mm tall, not obviously stipitate, the basal angles light orange, merging into the ovary, the style slender, erect, white, 10 mm long, apically clavate, slightly compressed, the stigma green forming a small, curved crest with a faint longitudinal suclus. *Fruits* bright red berries, loosely enfolded by the reddish, slightly enlarged calyx lobes. Nectar is secreted by the corolla throat in the regions between the filaments. Whether the basal angles of the ovary, which have been termed a nectary in other related groups, actually secrete nectar is not known.

This species has long been cultivated in European botanical gardens. It was described from plants grown in Goettingen from seed received from Mexico from Spangenberg. Somewhat after its 1832 publication by Schrader, Dunal (1852: 433) amplified the collection notes to "in sylvis alpinis Mexici." But no more recent material from Mexico has been seen by the present authors, although no search has been made beyond the Missouri Botanical Garden (MO). The plant was well figured by Sweet (1838: tab. 323), but as no recent figures or descriptions are known, an amplified description is provided here. This description differs from Dunal's in that the anthers are purple, and not really yellow, although the copious pollen gives dehisced anthers a yellowish cast. The filaments are actually subequal, with two opposing ones longer than the other three.

The name *Saracha* Ruiz & Pavon has been used in a mistaken sense until quite recently when Gentry (1973) pointed out that this name should be restricted to a group of South American trees and that the herbaceous plants hitherto known as *Saracha* should be referred to *Jaltomata* Schlecht. (1838). The plant at hand is clearly not congeneric with the South American plants properly called *Saracha*, but there is some question as to its correct placement. Quite similar to *Jaltomata procumbens* (Cav.) J. L. Gentry, the type species of *Jaltomata*, this species differs most importantly in its fasciculate rather than pedunculate inflorescence and in having narrow, nonflexing calyx lobes and saccate calyx angles. The two species, *J. procumbens* and *J. viscosa*, have similar anthers: there is a large connective visible on the dorsal side and a deep groove on the ventral side. A similar plant is *Physalis stapelioides* (Regel) Bitt. which has similar pubescence, leaf shape, solitary flowers, and large corollas. The calyx teeth are of the same shape as in *J. viscosa* but the calyx is not deeply lobed and does not turn red. *Physalis stapelioides*, which was first described under *Saracha*, appears to be a well-accommodated member of the genus *Physalis*, while *Saracha viscosa* has its closest affinities with *Jaltomata procumbens*. Menzel (1950) indicated that on cytological evidence, *Jaltomata procumbens* and *J. viscosa* are more like one another than they are to any of the several species of *Physalis* she examined.

Lycianthes santaeclarae (Greenman) D'Arcy, comb. nov.

Solanum sanctaeclarae Greenman, Bot. Gaz. (Crawfordsville) 27: 211. 1904. TYPE: Costa Rica, *Donnell Smith 6783* (F).

This species is distinctive in its globose, truncate, accrescent calyx which is vestite with brown, stellate hairs. It has recently been collected in Panama: El Llano-Cartí Road, 23.4 km from Interamerican Highway in wet forest, *Mori*

& Kallunki 5581 (MO). The collectors note that this is an epiphytic shrub with purple petals. It was in bloom and young fruit in mid April, 1975.

Nicotiana cutleri D'Arcy, sp. nov.

Herba granda, ramis puberulentibus, foliis glabratis, corollis rectis, parvis, glabratis, calycibus tomentulosis.

Herbs 40–60 cm tall; stems terete with 1–2 shallow furrows, tomentulose with short-stalked glandular and eglandular trichomes. *Leaves* chartaceous, cordate, to 15 cm long, 8 cm wide, apically obtuse, basally cordate on the lower leaves, obtuse on those in the inflorescence, the margin subentire to repand, the veins ca. 6 on each side, the blade glabrate to minutely puberulent, the veins puberulent; petiole unwinged, to 4–5 cm long, pubescent. *Inflorescences* narrow, thrysiform, many flowered; peduncle stout, becoming slender and angled apically, 20–40 cm long, the basal branches subtended by reduced leaves, the apical branches ebracteate or with pubescent, narrow leaves; pedicels to 5 mm long, tomentulose. *Flowers* with the calyx 6 mm long, tubular-campanulate with 5 narrowly deltoid teeth, outside evenly tomentulose overall, minutely puberulent inside; corolla urceolate-tubular, 17 mm long, 6 mm wide, straight, the throat cylindrical to ellipsoidal, strongly contracted apically and basally, the limb with 5 sinuate lobes ca. 2 mm long, glabrous outside except for a few hairs at the apex, glabrous inside; stamens included, 5, inserted ca. 3 mm above the base of the corolla tube, the anthers clustered just below the corolla mouth, 3 mm long, ovate, the filaments ca. 12 mm long, the basal 4–5 mm thickened and long pilose, the apical ⅔ glabrous, slender; ovary narrowly ovate, ca. 3 mm long, the style cylindrical, the apical 6 mm puberulent, glabrous below, the style compressed, slightly 2-lobed. *Fruits* not seen.

TYPE: BOLIVIA. DEPT. TARIJA: Between Las Carreras and Escayachi, 200 m, clayish soil on river bank, flower yellow greenish, *Cardenas 4948* (MO, holotype; BIRM, isotype).

This species is a member of subgen. *Rustica,* sect. *Paniculatae* Goodsp. It is similar to *N. paniculata* L., but has less pubescent leaves, much smaller flowers, and no expansion of the corolla limb in the region of the anthers. It is also well outside the distributional range of *N. paniculata* which Goodspeed (1954) recorded as endemic to Peru. *Nicotiana cutleri* is also reminiscent of *N. knightiana* Goodsp., another Peruvian endemic, which has a conspicuously pubescent corolla, and of *Nicotiana benavidesii* Goodsp. which has exserted stamens.

This species is named for Dr. Hugh Cutler, Missouri Botanical Garden, who transmitted the type specimen from M. Cardenas, collector of the type.

Solanum stramoniifolium Jacq., Misc. Aust. 2: 298: 1781; Ic. Pl. Rar. 1: 44. 1782. TYPE: *Jacquin* (W).

This species is common in disturbed vegetation in the lowlands of northern South America but has hitherto not been recorded from Panama. Mr. Michael Nee, University of Wisconsin, and important contributor to collection of the

Panamanian flora, was the first to locate this plant on the lowland, coastal strip of Bocas del Toro Province.

Solanum stramoniifolium is a member of sect. *Lasicarpum*. The leaves closely resemble those of *Solanum hirtum* Vahl, with which this species has been confused in the past, and it has similar acicular spines. The calyx of this species, however, is short and the five lobes are truncate with short sinuses. In living material, secretions from the five nectaries stand out as conspicuous clear beads. In the recent treatment of the Solanaceae in the *Flora of Panama* (D'Arcy, 1973) this species would key out on p. 691 under "d" along with *S. hirtum*. The structure of the calyx lobes is the best distinction here, as *S. hirtum* has large, subfoliaceous, deltoid calyx lobes. The pubescence of *S. stramoniifolium* is much finer and there is more tendency for spines on lower parts of the stem to recurve.

Witheringia exiguiflora D'Arcy, sp. nov.—FIG. 1.

Frutex glaber, foliis grandis, obliquis, aniso-geminatis, inflorescentibus fasciculatis, floribus parvis, corollis intus glabris, antherae nunc apiculatis nunc calvis, calyce accrescenti, acinum involventi.

Glabrous *shrubs* to 3 m tall; twigs stout, drying wrinkled. *Leaves* prominently aniso-geminate; major leaves elliptical, oblique, to 40 cm long, 15 cm wide, apically acute or acuminate, basally rounded, obtuse or sometimes somewhat dimidiate, the veins 14–18 on each side of the midvein, on the broader side parallel, on the smaller side arcuate, the petiole to 17 mm long; minor leaves rotund, to 5 cm long, veins 4–5 on each side, the petioles mostly less than 1.5 mm long. *Inflorescences* few- to several-flowered fascicles in the leaf axils; pedicels to 5 mm long, glabrous, drying angled. *Flowers* with the buds ellipsoidal, 10–15 mm long, 5 mm across; calyx lobes free or fused, the calyx tubular, apically truncate or sinuate with 2–5 angles in the upper portion sometimes forming short umbos or subfoliaceous teeth, glabrous or pubescent with simple hairs, the sinuses hyaline, splitting on corolla egress, 3 mm long at anthesis but soon accrescent; corolla pale yellow, campanulate to tubular, to 17 mm long, glabrous or minutely puberulent outside, glabrous within, the sinuses splitting about halfway down to form 5 lobes; stamens 5, inserted 4 mm from the base of the tube, 4 mm below the lowest corolla sinus, the filaments free 4 mm, glabrous or with a few hairs just above the point of insertion, the anthers oblong, 3.5 mm long, basifixed and basally auriculate, apiculate or not, included, only partly exceeding the corolla sinuses; ovary narrowly pyramidal with rounded angles, apically truncate, ca. 3 mm tall, 1.3 mm broad, the nectary 0.6 mm tall but inconspicuous and merging with the contours of the ovary, the style uniformly cylindrical, glabrous, the stigma capitate, small, faintly 2-lobed, not exceeding the anthers. *Berry* enclosed by the accrescent calyx which is narrowly pyriform or elliptical, ca. 15 mm long, apically exceeding the berry and the lobes free; seeds dark, discoid, muricate, ca. 2 mm in diameter.

TYPE: PANAMA. PANAMA: 16 km N of Panamerican Highway on the Llano-Cartí Road, premontane wet forest, 400–450 m, *Nee & Dressler 9340* (MO, holotype).

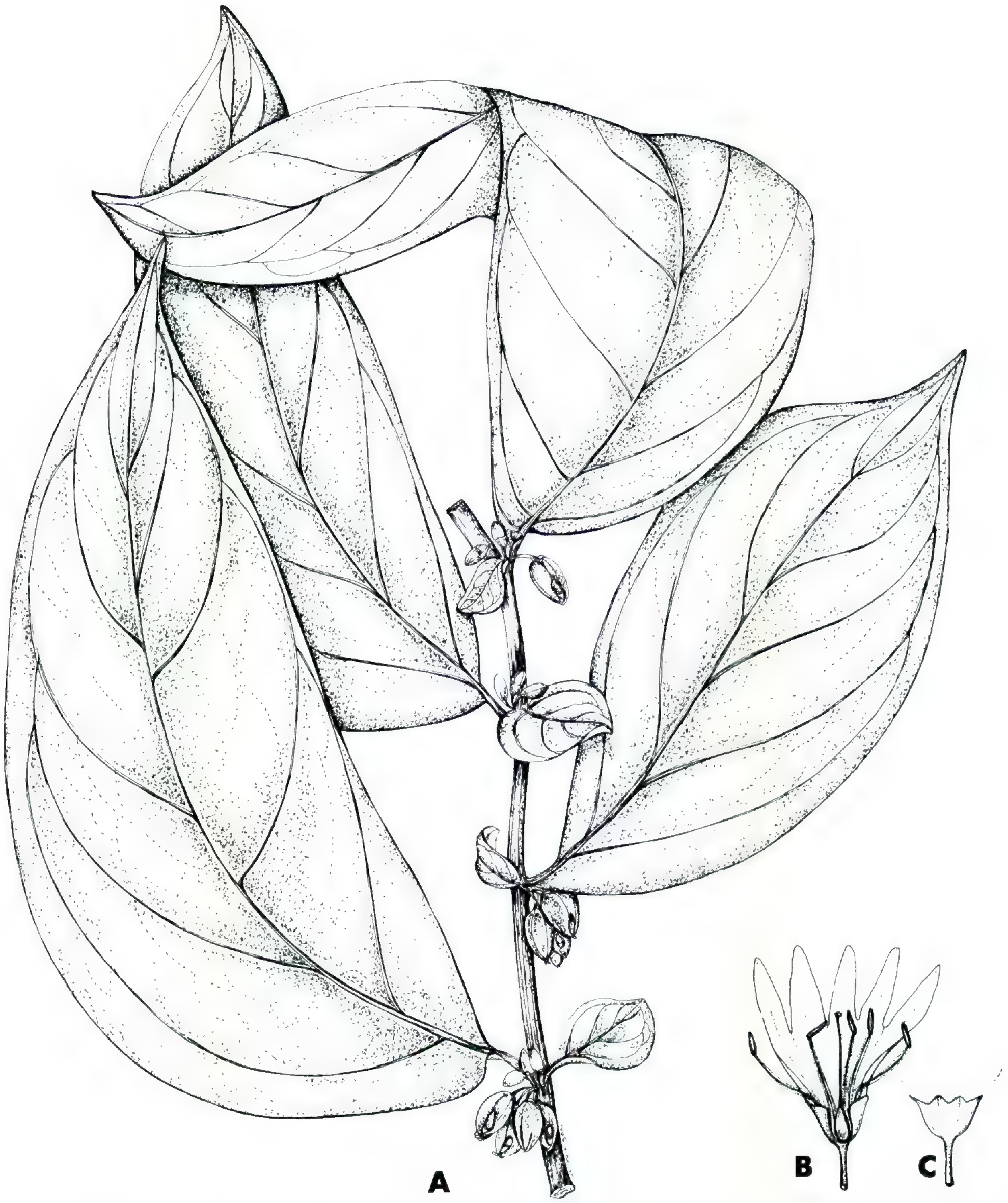

FIGURE 1. *Witheringia exiguiflora* D'Arcy.—A. Habit with fruits in fascicles at the nodes (×½).—B. Opened flower showing gynoecium and androecium (×2).—C. Calyx (×2). [After *Dressler 4582* (MO).]

Additional collections examined: COSTA RICA. CARTAGO: Río Chitaria crossing of Highway 10, 5 km E of Turrialba, 850 m, *Haber RC-1* (MO). LIMÓN: Valle of Río Sapo, 7 km S of Siquirres, Valle Escondido, 750 m, *Haber VE-4, VE-8* (both MO).

PANAMA. DARIÉN: Near upper gold mining camp of Tyler Kittredge on headwaters of Río Tuquesa, ca. 2 air km from Continental Divide, *Croat 27244* (MO). Cerro Campamento, S of Cerro Pirré, *Duke 15653* (MO). Top of Cerro Mali, 1300–1420 m, *Gentry & Mori 13639* (MO). Caná-Cuasí Trail, Chepigana District, 200 ft, *Terry & Terry 1611* (A). PANAMÁ: 20–21 km N of El Llano on El Llano-Cartí Highway, *Dressler 4582* (MO). 16 km above Panamerican Highway on road to Cartí, 400 m, *Kennedy 2684* (MO). SAN BLAS: Forest SW of Puerto Obaldía, *Croat 16836* (MO).

Although this species has been collected a number of times, most collections consist mainly of leaf and stem with little in the way of flower or fruit. The large, oblique, aniso-geminate leaves which are sometimes coriaceous, and the stems which appear stout and weak and dry with longitudinal wrinkles are quite unusual in the Panamanian flora. Flowers vary considerably, the calyx in most collections being quite glabrous but in *Dressler 4582*, the young calyx is pubescent and in *Terry & Terry 1611* it is tomentose. Calyx prefloration is complete or valvate-imbricate in different elements of *Nee & Dressler 9340*. In fruit the calyx envelops the berry and the lobes are sometimes slightly expanded beyond it. The fruit is directed downwards and sometimes the flowers are nodding too. In no collection seen is there any evidence of splitting of the fruiting calyx.

The generic affinities of *Witheringia exiguiflora* are by no means clear, although it seems most closely related to *Witheringia riparia* H.B.K. which occurs at upper elevations in Central America and in northern South America. In both of these species the calyx is accrescent; in *W. riparia* it is shorter than the berry and on herbarium sheets is often split lengthwise for at least part of its length. The corolla tube of *W. riparia* is quite pubescent at the point of stamen insertion whereas in *W. exiguiflora* it is glabrous.

Collections of *Witheringia exiguiflora* all come from premontane wet or rain forests, presumably between 300 and 1,500 m elevation. The flora of this ecological confine has been poorly sampled to date, and future collections may indicate a somewhat different regional distribution from that now indicated. Habitat reflecting the temperature and moisture parameters of this ecological regime extends as a narrow strip from Guatemala to Peru and Venezuela, and collections may be expected from any point along this strip, even though present information requires listing the species as endemic to Panama and Costa Rica.

Witheringia morii D'Arcy, sp. nov.

Witheringia morii D'Arcy, spec. nov. Frutex glaber, foliis aniso-geminatis, grandis, inflorescentibus floridis, fasciculatis e axillis foliorum, floribus parvis, corolla extus puberulenti intus sparsim tomentosa, calyce fructiferi leviter accrescenti.

Shrubs to 1 m tall; twigs glabrous, appearing soft, relatively stout, drying wrinkled or smooth. *Leaves* conspicuously aniso-geminate; major leaves elliptic, oblique, to 30 cm long, 10 cm wide, apically acuminate, basally acute with ca. 8 prominent, arcuate veins on each side, glabrous, the petioles ca. 10 mm long, wingless; minor leaves elliptic, oblique, 4–8 cm long, the petioles to 3 mm long. *Inflorescences* many-flowered fascicles in the leaf axils; bracts resembling reduced minor leaves; pedicels 2–5 mm long, glabrous. *Flowers* drying reddish brown, the buds globose; calyx prefloration nearly complete with only a pore present, the calyx glabrous, becoming 5 mm long in flower, splitting at the sutures but apical teeth or basal umbos not produced; corolla campanulate, 15–18 mm long, exserted ca. 10 mm from the calyx, the membranous sutures splitting more than halfway down to form 5 lobes, the lobes apically puberulent outside with degenerate trichomes, inside pubescent in tufts just below the point of stamen insertion; stamens 5, inserted ca. 4 mm from the bottom of the corolla tube, ca. 1.5 mm below the sinuses, the filaments compressed, glabrous, the anthers nar-

rowly hastate, 3 mm long, basifixed, basally 1 mm across, not apiculate, the tips only slightly exceeding the corolla sinuses; stigma subcapitate, the apical portion of the style somewhat expanded, the ovary not examined. *Fruits* not seen.

TYPE: PANAMA. CHIRIQUÍ: Coffee finca of Rattibor Hartman, "Ojo de Agua," 27 km NW of El Hato de Volcán, Santa Clara region, 5000–5300 ft, *Mori & Bolten 7192* (MO, holotype).

Additional collections examined: COSTA RICA. PUNTARENAS: Premontane rain forest, Finca Las Cruces Field Station 5 km S of San Vito on Highway 16, 1200 m, *Haber SV-15* (MO).

This species is singular in its large, aniso-geminate leaves and in its flowers. The calyx is similar to that of *W. riparia* H.B.K., but the corolla becomes deeply lobed and the anthers are not apiculate.

Although the two known collections are from different countries, the two localities are only some 25 km apart, have similar rainfall and temperature regimes, and do not differ more than 400 m in elevation.

LITERATURE CITED

D'ARCY, W. G. 1973. Solanaceae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 60: 573–780.

DUNAL, M. F. 1852. Solanaceae. *In* A. P. de Candolle, Prodromus Systematis Naturalis Regni Vegetabilis. Vol. 13(1): 1–690.

GENTRY, J. L., JR. 1973. Restoration of the genus *Jaltoma* (Solanaceae). Phytologia 27: 286–288.

GOODSPEED, T. H. 1954. The Genus *Nicotiana*. Chronica Botanico Co., Waltham, Massachusetts.

MENZEL, M. Y. 1950. Cytotaxonomic observations on some genera of the Solanae: *Margaranthus*, *Saracha*, and *Quincula*. Amer. J. Bot. 37: 25–30.

SWEET, R. 1838 (1836). The British Flower Garden. Ser. 2. Vol. 4. James Ridgway and Sons, London.

A NEW PANAMANIAN *STERCULIA* WITH TAXONOMIC NOTES ON THE GENUS[1]

Alwyn H. Gentry[2]

Abstract

Sterculia glauca A. Gentry is newly described from Panama. It is most closely related to S. *guianensis* Sandw. All recognized species of tropical American *Sterculia* are arranged into species-groups on the basis of vegetative characteristics.

Sterculia glauca A. Gentry, sp. nov.

Species ab S. *guianensi* Sandw. foliis parvis ellipticis vel obovatis minus acuminatis, inflorescentiis subracemosis, gynophoris glabratis, differt.

Tree 15–25 m tall and 15–40 cm d.b.h. Leaves small, clustered toward tips of brachlets, elliptic to obovate, short-acuminate, rounded to cuneate at the base, 4–14 cm long, 2–6.5 cm wide, of varying sizes on each twig, entire, subcoriaceous, glabrous, drying brownish gray above, pale gray and almost glaucous below, the midvein prominent above and below, the secondary veins plane or slightly impressed above, prominent below, the tertiary venation slightly prominulous below; petiole 0.3–5.5 cm long, flattened above, glabrous. *Inflorescence* a raceme or racemose panicle, mostly clustered at the apex of branchlets, when not strictly racemose with only a few short 2-flowered lower primary branches, the pedicels and rachis pubescent with branched trichomes, the pedicels 3–4 mm long, the bracts and bracteoles subulate, minute, caducous. *Flowers* 7–10 mm long, the calyx 5-lobed, stellate pubescent outside and inside on apical 2–3 mm above a densely pubescent transverse appendage, also with scattered longer sparingly forked trichomes throughout; gynophore curved, the tip pendent, glabrous except for minute glandular trichomes at thickened base; male flowers with staminal tube pendulous, short and patelliform, glabrous, the anthers ca. 0.5 mm long; perfect flowers with ovary villous, the stigma peltate, the style pubescent and ca. 2 mm long. *Fruit* with the peduncle 13–15 cm long, the 5 apical follicles pedicellate, ellipsoid, not apiculate, 11–14 cm long, 7–8 cm in diameter, the pericarp woody, finely puberulous, ca. 1 cm thick, villous with urticating trichomes inside; seeds ellipsoid, ca. 3 cm long, ca. 1.3 cm in diameter.

Type: Panama. panama: El Llano-Cartí Road, 8.6 km from Interamerican Highway, 1100–1200 ft, wet forest, tree 15 m tall, 40 cm d.b.h., tepals yellow green outside, rose red inside, 27 Dec. 1974, *Mori, Kallunki & Hansen 4093* (MO, holotype; isotypes to be distributed).

Additional collections examined: Panama. panama: (El Llano-Cartí road near San Blas Border): 5–6 mi N of El Llano, 1300 ft., *Gentry* 5822 (MO, to be distributed). 8–12 km N of El Llano, 400–450 m, *Nee et al. 8806* (MO, PMA). 10–12 km N of Interamerican Highway, 410 m, *Mori & Kallunki 2884* (MO, to be distributed). colón: East Santa Rita Ridge, *Correa & Dressler 665* (MO).

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[1] I thank Ghillean Prance and A. J. G. H. Kostermans for reviewing the manuscript.

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Sterculia is in great need of monographic treatment and hence a difficult group to work with. Nevertheless the new Panamanian species is so distinct from all described species of the genus as to leave no doubt that it is indeed undescribed. It is very unusual in the genus in its completely glabrous leaves and whitish almost glaucous leaf undersurfaces.

Clearly *Sterculia* contains fewer species in tropical America than extant names, although no effort has been made to establish synonymies. Most species fall into relatively few species-groups on the basis of vegetative characteristics. Although I have made no effort to consult types, the affinities of most species are clear from their descriptions. The following groups may be recognized:[3]

1. *Sterculia mexicana* R. Br. and *S. laxiflora* Rusby—palmately compound leaves.

2. *Sterculia apetala* (Jacq.) Karst. (including *S. acerifolia* Hemsl., *S. carthaginensis* Cav. and *S. punctata* Moc. & Sessé ex DC.), *S. elata* Ducke, *S. striata* St.-Hil. & Naud., *S. chicha* St.-Hil., and *S. guaypayensis* Cuatr.—lobed leaves.

3. *Sterculia rugosa* R. Br., *S. costaricana* Pittier (including *S. recordiana* Standl.), *S. colombianum* Sprague, *S. pojoira* Cuatr., *S. stipulifera* Ducke, *S. pilosa* Ducke, *S. apeibophylla* Ducke, *S. rigidifolia* Ducke, *S. speciosa* K. Schum., *S. solitudinis* Mildbr., and *S. corrugata* Little—entire coriaceous leaves with prominent tertiary venation beneath; always with some stellate trichomes and usually strongly stellate pubescent beneath.

4. *Sterculia excelsa* Mart. (including *S. surinamensis* R. Br. and *S. villifera* Steud.)—similar to *S. rugosa* group but with leaves firmly membranous to chartaceous and venation less prominent beneath, conspicuously stellate pubescent; *S. guaypayensis* (see above) also said to be similar except for its somewhat lobed leaves.

5. *Sterculia pruriens* (Aubl.) K. Schum. (including *S. crinita* Cav., *S. ivira* Swartz and *S. propinqua* R. Br.), *S. tessmannii* Mildbr., *S. caribaea* R. Br., and *S. albidiflora* Ducke—leaves entire, chartaceous to subcoriaceous, distinctly but not conspicuously stellate puberulous beneath and along petioles, tertiary venation prominulous beneath.

6. *Sterculia frondosa* L. Rich., *S. glabrifolia* Mildbr., *S. roseiflora* Ducke, *S. venezuelensis* Pittier—leaves entire, chartaceous to subcoriaceous, glabrate, the

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[3] *Xylosterculia* Kostermans was recently (1973) proposed for *S. pilosa* and *S. rugosa*, based on a woodier "indehiscent" fruit lined with urticating hairs inside. This distinction seems unwarranted: all *Sterculia* fruits known to me are woody, dehiscent, and lined with stinging hairs (cf. Janzen, 1972). The two *Xylosterculia* species are very close to the other species of the *S. rugosa* group, several of which are known to be dehiscent; the fruit illustrated by Kostermans was obviously very immature when collected, and this is presumably responsible for its apparent indehiscence. Even were some *Sterculia* fruits indehiscent, the difference seems taxonomically unimportant in the genus: Janzen (1972) has noted that the only effective seed dispersal in dehiscent-fruited *S. apetala* occurs when undehisced fruits are removed from the tree. Dehiscence on the parent tree results in increased seed predation. In such a situation selection for delayed dehiscence or indehiscence would hardly represent the kind of fundamental change usually associated with generic differentiation. Pericarp thickness of the difference species ranges uninterruptedly from a few mm to the 2 cm cited by Kostermans. I accept Kostermans's transfer of *S. cubensis* to *Hildegardia*. *Sterculia oblongifolia* Moc. & Sessé ex DC. is a synonym of *Colea acuminata*. All other New World Sterculias have been accounted for here.

tertiary venation beneath prominulous or scarcely evident. *Sterculia albidiflora* (see *S. pruriens* group above) was described as of this alliance, but specimens I have seen have a sparse tomentum of stellate trichomes beneath. The species of this group are all characterized by small (calyx 5–6 mm long) flowers and may prove to constitute a single species. Although *S. glabrifolia* Mildbr. (1927) is a later homonym of *S. glabrifolia* Merrill (1920), I refrain from proposing a *nomen novum* in expectation that it may prove synonymous with *S. frondosa*.

7. Miscellaneous—*Sterculia megalocarpa* A. C. Smith seems intermediate between the *S. rugosa* group and the *S. pruriens* group. *Sterculia pendula*, likewise stellate pubescent below, may also be related to the *S. pruriens* group. No material of these two species has been seen. The final three species of the genus —*S. aerisperma* Cuatr., *S. diguense* Cuatr., and *S. guianensis* Sandw.—are closest to *S. glauca*, agreeing in glabrate leaves and relatively large flowers (calyx ca. 1 cm long). *Sterculia aerisperma* differs in smaller, laterally compressed and pointed follicles and the leaves are not at all glaucescent beneath. *Sterculia diguense* (flowers not known) has a fruit very similar to that of *S. glauca* but very different much larger leaves which are minutely tomentellous below; it is probably allied to the *S. rugosa* group. The final species, *Sterculia guianensis* of Guyana, is perhaps the closest relative of *S. glauca*. It agrees in glabrate acuminate leaves rounded to almost cuneate at the base and with inconspicuous tertiary venation below, as well as subracemose inflorescence and similar flower size (flower 1.2–1.6 cm long, calyx lobes 7–11 mm long). Its leaves are described as pale and almost glaucescent beneath, the only species sharing this feature with the Panamanian plant.

Should *S. glauca* be separated from *S. guianensis*? That species differs noticeably in the lanceolate shape of its much longer leaves (11–33.5 cm long, 3.5–9.5 cm wide), longer (1–1.5 cm) leaf acumen, and its pedicels are longer (7–5 mm versus 3–5 mm). The gynophore is furfuraceous rather than glabrous. The flowers of *S. guianensis* are also slightly larger and the bracts to 7 mm long. *Sterculia glauca* is adequately separated but joins the growing list of eastern Panamanian species with their closest relatives in Guayana (cf. Gentry, 1975).

LITERATURE CITED

GENTRY, A. H. 1975. Additional Panamanian Myristicaceae. Ann. Missouri Bot. Gard. 62: 474–479.

JANZEN, D. H. 1972. Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. Ecology 53: 350–361.

KOSTERMANS, A. J. G. H. 1973. Some new taxa. Bot. Tidsskr. 67: 317–319.

NOTES

RHYNCHOSTEGIOPSIS CAROLAE (MUSCI, HOOKERIACEAE): A NEW SPECIES FROM COSTA RICA

Rhynchostegiopsis carolae Crosby, sp. nov.—Figs. 1–5.

Differt haec species a *R. complanata* C. Müll. cellulis apicalibus marginalibus minus inflatus.

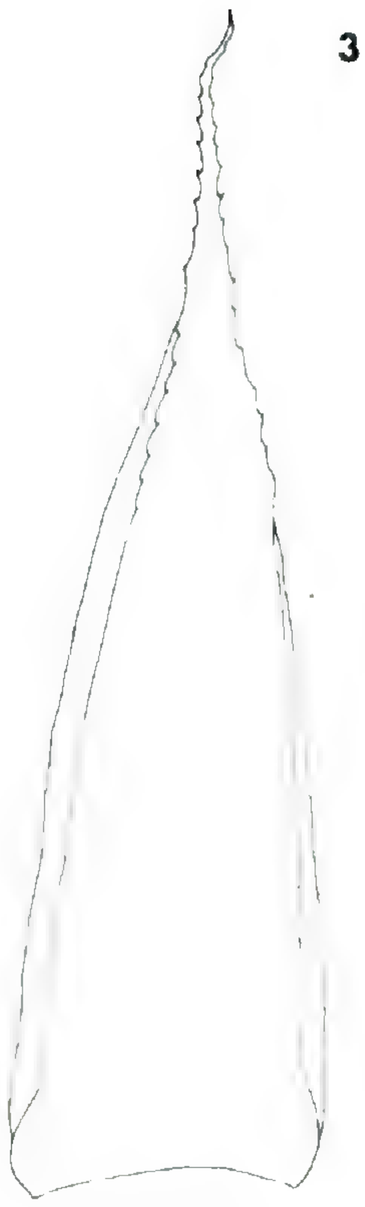
Plants robust, stems often 10–12 cm long before decaying and breaking up, infrequently subpinnately branched, foliated stems and branches 5–7 mm wide. Leaves 5.0–6.0 × 1.5–2.0 mm, dorsals ovate, gradually narrowed to short acumen (Fig. 3), laterals falcate, often folded (Fig. 4), ventrals usually wider and slightly falcate (Fig. 5); margins entire below, serrate in acumen; marginal cells at widest point of leaf 6–8 μm wide and the submarginal 4–6 rows of cells conspicuously narrower (6–10 μm wide) than median cells, marginal cells in acumen not or slightly inflated (Fig. 1), median cells 200–300 × 12–18 (–30) μm (Fig. 2), basal cells 100–120 × 20–30 μm. Dioicous. Perichaetial leaves 1.5–2.2 × 0.8–1.0 mm, mostly broadly ovate with gradually acuminate, entire apices. Perigonial leaves 0.8–1.4 × 0.4–0.5 mm, mostly ovate with gradually acuminate, entire apices. Seta 1.6–3.7 cm, deoperculate capsules 1.5–2.0 × 0.8–1.0 mm, operculum 1.4–1.6 mm long, the beak 1.0–1.1 mm.

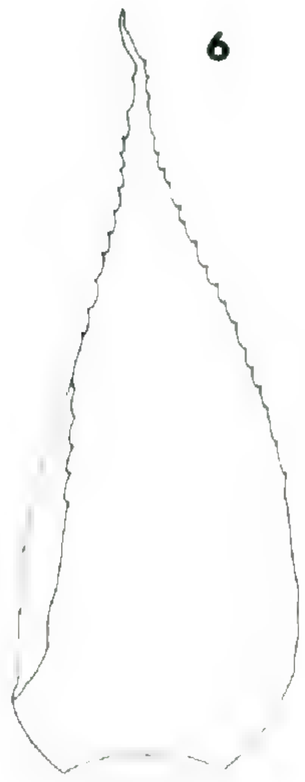
Type: Costa Rica. prov. san josé: Along Inter-American Highway, 13 km SE of El Empalme, 9.40 N, 83.51 W, 2600 m, *Marshall R. & Carol A. Crosby 5836* (MO, holotype; BA, BM, CR, DUKE, H, MICH, NICH, U, isotypes).

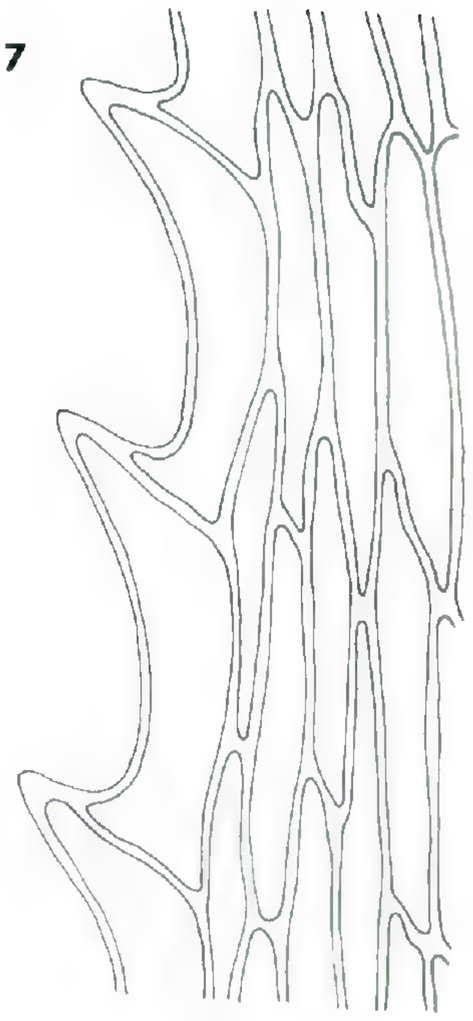
Additional specimens: Costa Rica. prov. cartago: Dos Amigos area, near km 73 marker on Inter-American Highway, *Crosby & Crosby 5957* (MO). prov. heredia: SW slopes of Volcán Barba, *Crosby 3704* (BA, CR, DUKE, FH, H, NICH, U). Las Vueltas area, Río Patria, 18 km N of San José, *Crosby & Crosby 6005* (B, CR, MO), *6608*, *8523* (both MO). prov. san josé: W side of Inter-American Highway, 17 km SE of El Empalme, *Crosby 9761* (CR, H, MO), *9766* (MO), *10861* (CAMN, CHR, COLO, CR, FH, FLAS, IJ, L, LE, MEXU, MICH, MO, NAM, PAC, PC, PMA, S, SP, TNS, U, US).

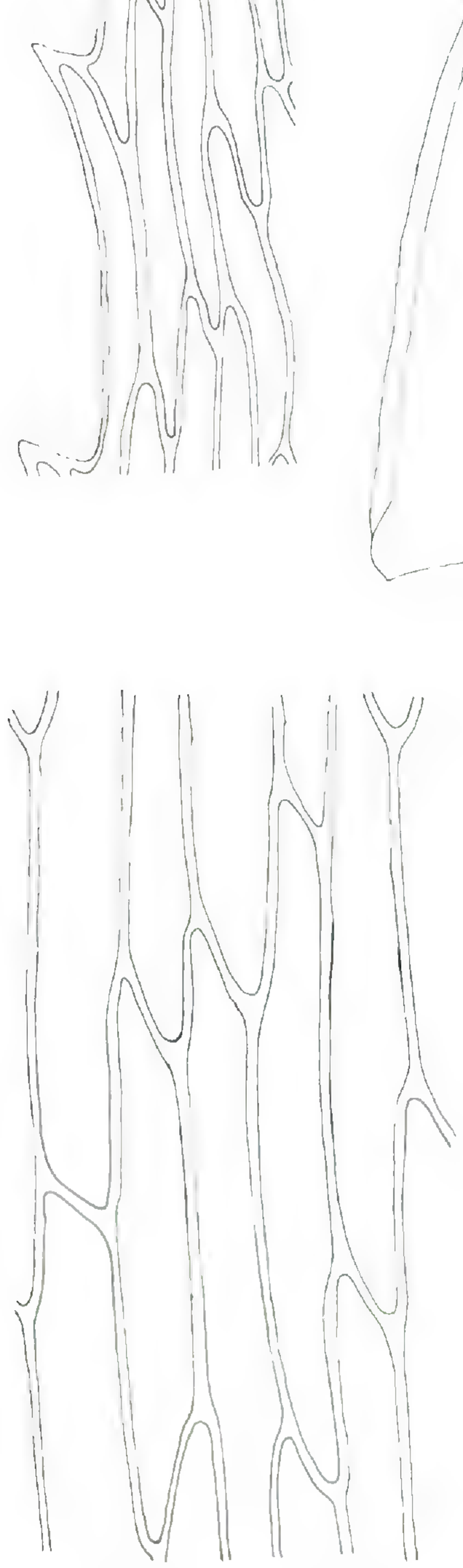
Rhynchostegiopsis carolae is a large, fairly common moss in middle (2,100–2,680 m) elevations in central Costa Rica, but it apparently has gone undescribed. Welch (1976) treats only *R. flexuosa* (Sull.) C. Müll. as occurring in Central America. Robinson & Griffin (1975) have described *R. costaricensis*, a distinctive species which usually bears propagula on the dorsal surface of the leaves. *Rhynchostegiopsis complanata* C. Müll, the species to which *R. carolae* is most similar, occurs in Bolivia.

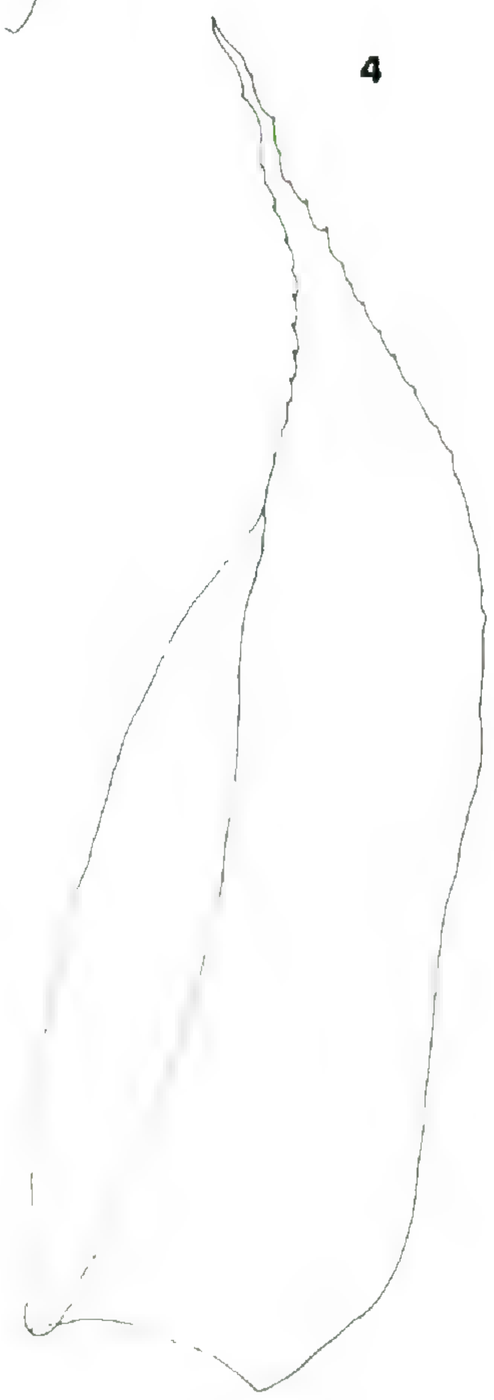
The distinctive features of *Rhynchostegiopsis carolae* are its large size coupled with the not or slightly inflated marginal cells in the apex of the leaves. The leaves of *R. complanata* (Bolivia, *Herzog 4025*, MO) are nearly as large, about 3 × 1 mm (Fig. 6), but the marginal apical leaf cells are greatly inflated, the leaf being coarsely serrate apically (Fig. 7). *Rhynchostegiopsis costaricensis* occurs sympatrically with *R. carolae* (*Crosby 9754*, CR, MO), but the much smaller

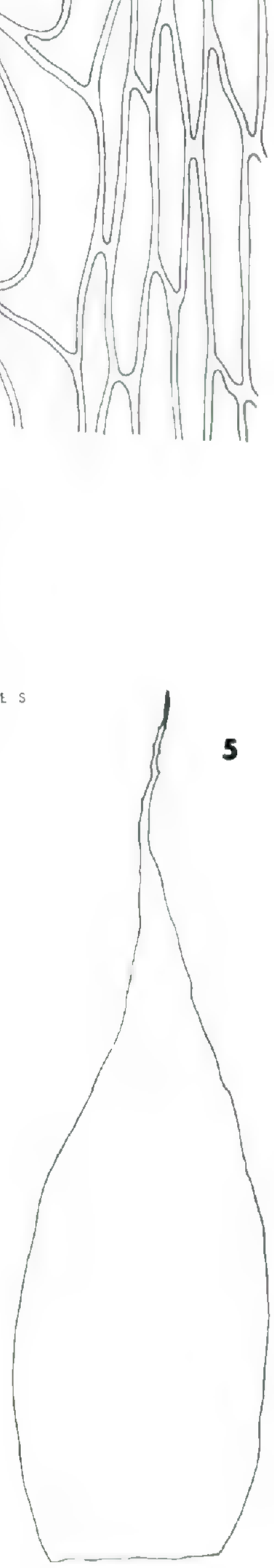












FIGURES 1–7. *Rhynchostegiopsis*.—1–5. *R. carolae*.—1. Apical marginal leaf cells.—2. Median leaf cells.—3. Dorsal leaf.—4. Lateral leaf.—5. Ventral leaf. [1–5 after *Crosby & Crosby 5836* (MO).]—6–7. *R. complanata*.—6. Dorsal leaf.—7. Apical marginal leaf cells. [6–7 after *Herzog 4025* (MO).]

leaves (2.0–3.0 × 0.5–0.8), inflated marginal cells in the apex, shorter seta (ca. 1.5 cm), and shorter operculum (ca. 1 mm) make it easy to distinguish. *Rhynchostegiopsis flexuosa* as treated by Welch is also much smaller with leaves 1.0–2.5 × 0.2–0.6 mm with more or less filiform, flexuous apices.

Supported by National Science Foundation Grant GB-43656.

Literature Cited

Robinson, H. & D. Griffin, III. 1975. A new species of *Rhynchostegiopsis* from Costa Rica (Hookeriaceae, Musci). Phytologia 30: 281–283.
Welch, W. H. 1976. Hookeriaceae. N. Amer. Fl., ser. 2, 9: 1–133.

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A NEW GYPSOPHILOUS SPECIES OF *GAILLARDIA* (ASTERACEAE) FROM CHIHUAHUA, MEXICO

Recent studies have led to the discovery of a number of new taxa endemic to gypseous soils in the southwestern United States and northern Mexico. Two gypsophilic species of *Gaillardia*, *G. gypsophila* and *G. powellii*, have already been described (Turner, 1972), and the species described here represents still another.

Gaillardia turneri Averett & Powell, sp. nov.—Fig. 1.

Herba perennis ad 3 dm alta ab caudex lignosa bene evoluta. Folia conspicue punctata leviter pubescentia.

Herbaceous perennial 30–75 cm tall, from a well-developed woody caudex. Stems erect, 20–50 cm long, leafy towards the base, striate. Leaves 5–7 cm long, 0.5–1.5 cm wide, the basal leaves with petioles 3–10 cm long, the upper leaves sessile or subsessile, pinnatifid, conspicuously punctate, glabrous or only slightly pubescent with soft white hairs. Involucre hemispheric 1.0–1.5 cm across, ca. 1 cm high; bracts in 2 series, ovate-lanceolate, 5–12 mm long, 1–2 mm wide, reflexed after flowering, villous. Receptacle convex, ca. 2 mm across and 1 mm high, with setae ca. 1 mm long. Ray florets 8, sterile; ligules yellow, ca. 1 cm long, 3–6 mm wide, 3-lobed, the lobes ca. 5 mm long. Disc florets numerous, collectively brownish-purple, the tube short, ca. 1 mm long, abruptly flaring into a tubular throat ca. 4 mm long, 1.0–1.5 mm wide; lobes short, acute, ca. 0.5 mm long, pubescent with purplish hairs. Achenes 2 mm long, densely pubescent with hairs extending beyond the achene. Pappus scales 10–12, ovate-lanceolate, attenuate into an awn, ca. 6 mm including a 3 mm awn. Chromosome number $n = 17$.

Type: Mexico. chihuahua: Gypsum outcrops, 6.6 mi E of Hwy. 16 on road to new lake on Río Conchos, 6 Apr. 1971, *A. M. Powell et al. 2025* (TEX, holotype; isotypes to be distributed).

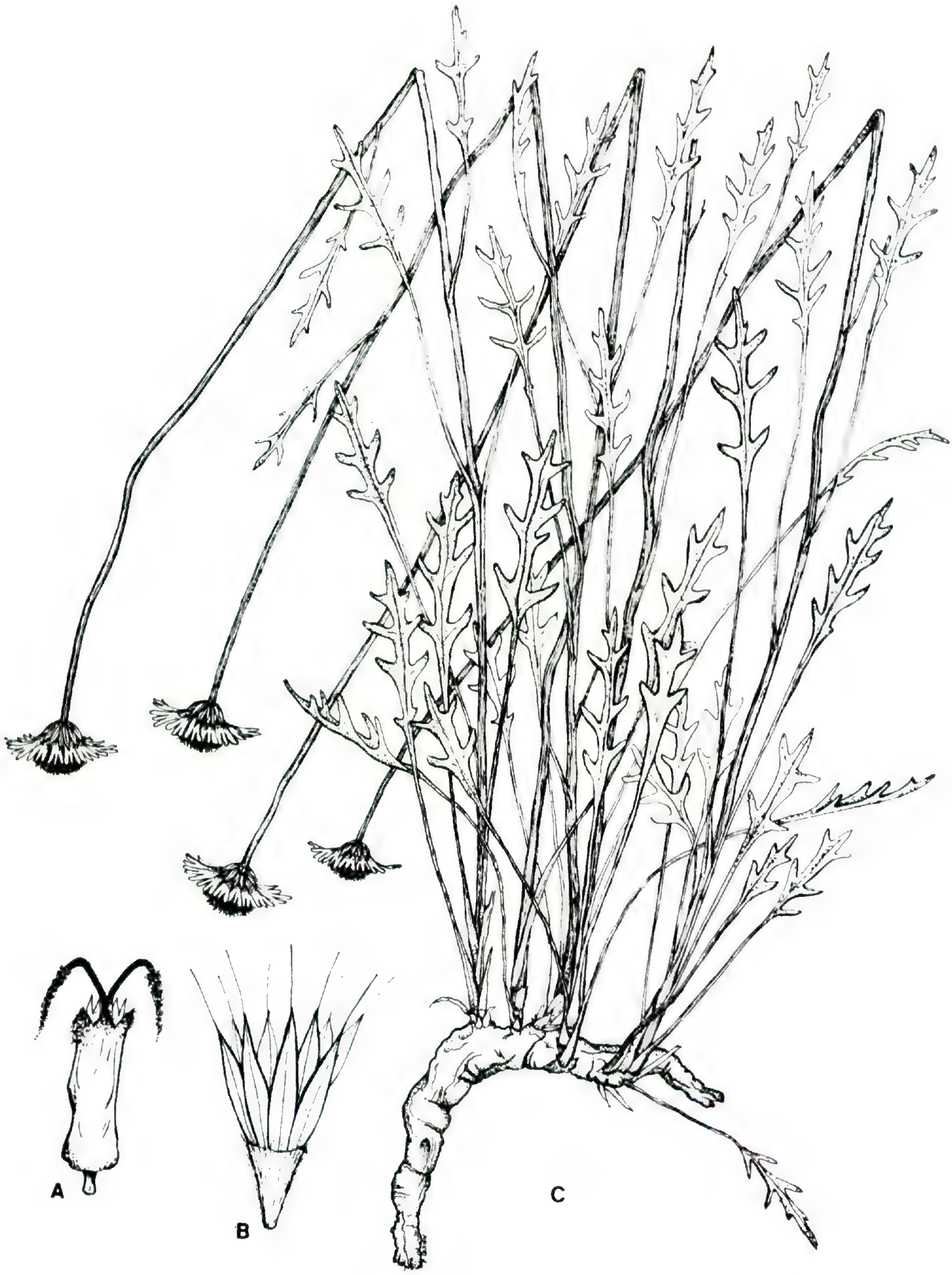

FIGURE 1. *Gaillardia turneri* Averett & Powell.—A. Disc floret.—B. Achene.—C. Habit. [After *Powell et al. 2025*, holotype (TEX).]

Gaillardia turneri is a diploid species closely related to *G. pinnatifida* but differs from the latter in its robust habit, woody caudex, and proclivity for gypsum habitats. Qualitative differences are apparent in the leaf vesture of the two species. The leaves of *G. pinnatifida* are more pubescent with less conspicuous

punctations than are the leaves of *G. turneri*. In support of the morphological distinctions, the two species also differ in their flavonoid complements (Averett, unpublished). The specific epithet honors Prof. B. L. Turner, University of Texas at Austin.

This work was supported in part by a Sigma Xi grant and a NSF grant (GB-37674).

Literature Cited

Turner, B. L. 1972. Two new gypsophilous species of *Gaillardia* (Compositae) from north-central Mexico. Southwest. Naturalist 17: 181–190.

—*John E. Averett, Department of Biology, University of Missouri-St. Louis, St. Louis, Missouri 63121 and Missouri Botanical Garden* and *Michael Powell, Department of Biology, Sul Ross State University, Alpine, Texas 79830.*

CHROMOSOME COUNTS IN *SOLANUM*

Solanum fosbergianum D'Arcy. $n = 12$. Panama. panama province: Finca del Indio, Cerro Jefe, *D'Arcy 5224* (MO); cultivated progeny, *D'Arcy 5224A* (MO).

Solanum sp. $n = 12$. Rwanda. Parc des Volcans, Karisimbe-Visoke Saddle, 3000 m, *D'Arcy 7587* (MO); cultivated progeny, *D'Arcy 7587A* (MO). This species has been known as S. *nigrum* L. in the mountains of East Africa. It exhibits considerable variability throughout the Virunga Volcanoes, but all plants of sect. *Solanum* in the area appeared to be the same taxon. They are more pubescent with longer hairs on the pedicels and of more scandent habit than plants of S. *nigrum* observed from Europe or from the northwestern United States, but it was not possible to make a clear taxonomic separation between the Virunga plants and those of S. *nigrum* from elsewhere within the study period. Current taxonomic practice (Stebbins & Paddock, 1949; Heiser, 1955, 1963; Baylis, 1958; Edmonds, 1972; D'Arcy, 1974) is to restrict the name S. *nigrum* to plants with the hexaploid chromosome number $n = 36$. At least six species of sect. *Solanum* have been described from the mountains of East Africa: S. *pentagonocalyx* Bitt., S. *kifinikense* Bitt., S. *subuniflorum* Bitt., S. *tarderemotum* Bitt. (all 1912); S. *hirtulum* Steud. ex Bitt. (1917), and S. *viridimaculatum* Gilli (1973). It is quite possible that one of these names applies to a diploid plant of the same species as that studied here. Because it has not been possible at this time to see appropriate types or ascertain the cytological condition of the sect. *Solanum* taxa of other African Mountains, the assignment of names to the Virunga populations must wait further studies.

Literature Cited

Baylis, G. T. S. 1958. A cytogenetical study of the New Zealand forms of *Solanum nigrum* L., S. *nodiflorum* Jacq., and S. *gracile* Otto. Trans. Roy. Soc. New Zealand 85: 379–385.

D'Arcy, W. G. 1974. *Solanum* and its close relatives in Florida. Ann. Missouri Bot. Gard. 61: 819–867.

EDMONDS, J. M. 1972. A synopsis of the taxonomy of *Solanum* sect. *Solanum* (Maurella) in South America. Kew Bull. 27: 95–114.
HEISER, C. B., JR. 1955. The *Solanum nigrum* complex in Costa Rica. Ceiba 4: 293–299.
———. 1963. *Solanum* (Morella) in Ecuador. Ci. & Nat. 6: 50–58.
STEBBINS, G. L. & E. F. PADDOCK. 1949. The *Solanum nigrum* complex in Pacific North America. Madroño 10: 70–81.

—W. G. D'Arcy, 2345 Tower Grove Avenue, Missouri Botanical Garden, St. Louis, Missouri 63110.

A NEW SPECIES OF *CHAMAESYCE* (EUPHORBIACEAE) FROM THE BAHAMAS

The recent surge of interest in the flora of the Bahama Islands has provided material from locations which are relatively poorly known botanically. Among collections from Inagua is a *Chamaesyce* which is distinct from anything previously described from the New World.

Chamaesyce proctorii Burch, sp. nov.

Herba perennis ex caudice; ramis supra tomentosis subtus glabris. Folia opposita; lamina ovata-oblonga, serrata; stipulae connatae, ciliatae. Cyathia solitaria; involucrum campanulatum; glandulae atropurpurae, appendices albae, crenatae. Capsula tomentosa, ovoidea; semina truncato-ovoidea, cineracea, parietibus rugosis.

Perennial herb, prostrate from a somewhat swollen rootstock, forming mats to 2 dm diam., usually with a red or purplish cast to all parts; stem to 0.5 mm diam., tomentose on the upper surface, branching throughout but with most laterals condensed, not rooting at the nodes. Leaves coriaceous; blade ovate-oblong, 6–8 mm long, 4–5 mm wide, the base oblique, the surface minutely papillate, variably tomentose, the margin coarsely serrate at least in the upper ⅓, the apex rounded to acute; petiole ca. 1 mm long; stipules joined at the base, triangular or somewhat bifid, densely ciliate particularly on the adaxial surface. Cyathia solitary at the nodes of condensed laterals, campanulate, to 1.2 mm diam. at the mouth, densely tomentose without, ciliate within; glands transversely elliptic, deep purple, the appendages white, equalling the glands, the margin deeply crenate; staminate flowers 12–18 per cyathia; ovary densely tomentose, the styles free to the base, bifid for half their length. Capsule densely tomentose or glabrescent, broadly ovoid, ca. 1.2 mm long and broad, scarcely lobed, the angles somewhat rounded; seed truncate-ovoid, to 0.8 mm long, 0.6 mm wide just above base, the ventral angle obscure, the others well marked, the faces convex, rugose, ashen.

TYPE: BAHAMAS. INAGUA: Vic. of Smith's Thatch Pond (also known as Lantern Head Pond), in shaded sandy soil, 18 Feb. 1973, *Proctor & Gillis 33336* (MO, holotype; GH, IJ, isotypes).

Additional collections: BAHAMAS. INAGUA: Beyond airport, 15 Jan. 1964, *Dunbar* 332 (BM). Beyond quarantine stations, 18 Feb. 1964, *Dunbar 376* (A, BM).

This species is easily distinguished from the other Bahamian taxa growing in limestone that share its reddish cast and papillose surface. All the varieties of *Chamaesyce lecheoides* (Millsp.) Millsp. have glabrous capsules, while the more northern *C. cayensis* (Millsp.) Millsp., which is pubescent, does not have the ciliate stipules of *C. proctorii.* The plant has a strong superficial resemblance to *C. helwigii* (Urb. & Ekm.) Burch, described from a single Haitian collection, but differs from this species in having smaller seeds, markedly ciliate stipules, denser short pubescence on the capsule, deep purple cyathial glands, and well-developed glandular appendages.

The epithet *proctorii* was chosen in recognition of the extensive contributions of Mr. George R. Proctor of the Institute of Jamaica to our knowledge of the flora of the whole Caribbean region.—*Derek Burch, Department of Biology, University of South Florida, Tampa, Florida 33620.*

CHROMOSOME COUNTS IN *GRIELUM* AND *CERCIS*

Grielum sinuatum L. $2n = 14$. SOUTH AFRICA. CAPE PROVINCE: Seed ex Kirstenbosch Botanic Garden and cult. Missouri Botanical Garden *Curtis 100* (MO).

The genus *Grielum* traditionally has been placed in the family Rosaceae (Bentham & Hooker, 1865: 625–626; Bremekamp & Obermeyer, 1935: 415–416; Thorne, 1968). *Grielum* and the closely allied genera *Neurada* (*N. procumbens* : $2n = 14$, Hagerup, 1932; Murín & Chaudhri, 1970) and *Neuradopsis* (uncounted) are generally placed in the subfamily Neuradoideae. The diploid chromosome number obtained from root tip squash preparations of *G. sinuatum* has been determined as $2n = 14$, offering additional confirmation of placement in the Neuradoideae. A previous report of *N. procumbens* : $2n = 12$ (Murbeck, 1916) is most likely incorrect, based on the count reported here and those discussed above. Erdtman (1952) concluded, based on a study of pollen morphology, that a close and singular relationship exists between *Grielum* and *Neurada* as compared to other members of the Rosaceae. However, Erdtman retained both genera in the Rosaceae. The external morphology of *Grielum* and *Neurada* are very similar (Bremekamp & Obermeyer, 1935) and suggest a relationship with the Rosoideae, as does the base chromosome number of $x = 7$ for Rosoideae. Takhtajan (1969: 223) and Merxmüller (1968) have accorded Neuradoideae family status, after Agardh (1858: 228), with Takhtajan suggesting that the family Neuradaceae is related to the subfamily Rosoideae. While elevation of the Neuradoideae to family status might seem a logical conclusion based on pollen morphology, external morphology and chromosome numbers do not seem to justify this change in rank, nor does such a change offer more valuable insight into the evolution or systematics of the group.

Cercis canadensis L. $n = 7$ U.S.A. native species, cult. Missouri Botanical Garden *Curtis 101* (MO).

Previously, both $n = 6$ (Senn, 1938) and $n = 7$ (Taylor, 1967) had been reported. The present report for *C. canadensis* is in keeping with those for other species in the genus—*C. occidentalis* : $2n = 14$ and *C. grifithii* : $2n = 14$ (Taylor, 1967)—strongly suggesting that the $n = 6$ determination is incorrect.

LITERATURE CITED

AGARDH, J. G. 1858. Theoria Systematis Plantarum, Accedit Familiarum Phanerogamarum. Vol. 1. Lund, Sweden.

BENTHAM, G. & J. D. HOOKER. 1865. Genera Plantarum. Vol. 1. Williams & Norgate, London.

BREMEKAMP, C. & A. OBERMEYER. 1935. Scientific results of the Vernay-lang Kalahari expedition, March to September, 1930. Sertum Kalahariense, a list of plants collected. Ann. Transvaal Mus. 16: 399–455.

ERDTMAN, G. 1952. Pollen Morphology and Plant Taxonomy. The Chronica Botanica Co., Waltham, Massachusetts.

HAGERUP, O. 1932. Über Polypolodie in beziehung zu Klima, Ökologia und Phylogenie: Chromosomenzahlen aus Timbuktu. Hereditas 16: 19–40.

MERXMÜLLER, H. 1968. Prodromus einer Flora von Südwestafrika. 56: Neuradaceae. J. Cramer, Germany.

MURBECK, S. 1916. Über die Organisation, Biologie und verwandtschaftlichen Beziehungen der Neuradoideen. Acta Univ. Lund 12(2): 1–29.

MURÍN, A. & I. I. CHAUDHRI. 1970. *In* IOPB chromosome number reports. XXVI. Taxon 19: 264–269.

SENN, H. A. 1938. Chromosome number relationships in the Leguminosae. Bibliogr. Genet. 12: 175–345.

TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Transl. by C. Jeffrey. Smithsonian Inst. Press, Washington, D.C.

TAYLOR, R. L. 1967. *In* IOPB chromosome number reports. XIII. Taxon 16: 445–461.

THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 4: 57–66.

—William F. Curtis, Department of Biology, Washington University, St. Louis, Missouri 63130.

NOMENCLATURAL CHANGES IN *ALNUS* (BETULACEAE)

The following names are published in advance of a revision of the American taxa of *Alnus*. Detailed discussions of these changes will be included in the larger work.

Alnus acuminata H.B.K. is a variable species occurring throughout much of mountainous Mexico, Central America, and South America. It is seen as consisting of the following subspecies in addition to the nominate one.

Alnus acuminata subsp. **arguta** (Schlechtendal) Furlow, comb. et stat. nov.

Betula arguta Schlechtendal, Linnaea 7: 139. 1832; *Alnus arguta* (Schlechtendal) Spach, Ann. Sci. Nat. Bot., sér. 2, 15: 205. 1841. TYPE: "Prope San Miguel del Soldado, Naulingo, Acatlán, et Chiconquiaco," *Schiede 21* (HAL?, not seen; MO!, isotype or isosyntype).

Alnus acuminata subsp. **glabrata** (Fernald) Furlow, comb. et stat. nov.

Alnus glabrata Fernald, Proc. Amer. Acad. Arts 40: 26. 1904. TYPE: Guanajuato, Mt. San Nicolás, 1882, *Dugés s.n.* (GH!, lectotype of Standley, Contr. U.S. Natl. Herb. 23: 168. 1920.).

Alnus jourllensis H.B.K. is usually said to differ from the other Latin American species in that its leaves are covered with crowded bright-yellow glands on the abaxial surface. Populations of such plants are not uncommon in central and southern Mexico, but these are not represented by Humboldt and Bonpland's type specimen in Paris, which instead corresponds to Fernald's *Alnus firmifolia*, having leaves bearing less conspicuous, smaller, darker, and more remote glands. The glandular form, which also differs from the typical in its more elliptically shaped leaves and more regular leaf lobes, and which occurs at lower elevations (generally below 2,500 m) is recognized as a new subspecies.

Alnus jorullensis subsp. **lutea** Furlow, subsp. nov.

A subspecie typica foliis anguste ellipticis, ovatis, vel obovatis ferentibus glanibus crebris luteis in pagina inferna distinguenda.

Distinguished from the typical subspecies by its narrowly elliptic, ovate, or obovate leaves bearing crowded yellow glands on the lower surface.

TYPE: MEXICO. MICHOACÁN: 8 km N of Uruapan along the roadside, 2,000 m, tree, 5 m high, trunk 15 cm in diameter, bark smooth with transverse constrictions, occasional, 28 Nov. 1971, *Furlow 330* (MSC!, holotype).

The species long called *Alnus maritima* Nuttall must be renamed because Nuttall failed to choose the earliest available epithet, *maritima*, from *Betula-alnus maritima* Marshall, instead basing his name on Muhlenberg's apparently independently derived manuscript name, *Alnus maritima*, referring to the same species. However, to reinstate Marshall's epithet now would create a later homonym of Nuttall's name. Therefore a new name, *Alnus metoporina*, derived from the Greek adjective μετοπωρινος (autumnal, referring to the autumn-blooming habit of the species) and based on Marshall's *Betula-alnus maritima*, is chosen. Since Marshall provided neither a Latin description or diagnosis nor a type specimen, a short diagnosis and a neotype are included.

Alnus metoporina Furlow, nom. nov.

Betula-alnus maritima Marshall, Arbust. Amer. 20. 1785. TYPE: U.S.A. DELAWARE: Sussex Co., 4 mi S of Milford on the W shore of Hudson's Pond, 14 Sept. 1970, *Furlow 205* (MSC!, neotype).

Alnus maritima Muhlenberg ex Nuttall, North Amer. Sylva 1: 50. 1842, nom. illeg. TYPE: *Muhlenberg 447*, without location or date (PH!, lectotype).

Differt a speciebus Americanis ceteris florescentia autumnali, amentis femineis solitariis in axillis foliorum summorum, foliis atrovirioribus, et venatione camptodroma.

It differs from the other American species by its autumnal flowering period, by its solitary female catkins in the axils of upper leaves, by its darker-green leaves, and by its camptodromous venation.—*John J. Furlow, Department of Biology, Capital University, Columbus, Ohio 43209.*

AN EARLIER NAME FOR *OENOTHERA STRIGOSA* (ONAGRACEAE)

The name *Oenothera villosa*, published by Carl Peter Thunberg in his *Prodromus plantarum Capensium* . . . in 1794, apparently has not been taken up subsequently. It can, however, be typified by an authentic specimen in the Thunberg herbarium, Stockholm, labeled "e Cap. b. Spei Thunberg," mentioned by Juel (1918: 251). This specimen is identical with the taxon treated by Munz (1965: 136) as *Oenothera strigosa* (Rydb.) Mack. & Bush subsp. *canovirens* (Steele) Munz, and not *O. mollissima* L. as supposed by Munz (1935: 659). This entity occurs mainly in the Great Plains region of North America east to the Ohio Valley and Michigan and is rare and, according to Munz (1965: 136), probably introduced sporadically eastward to the Atlantic seaboard.

It is difficult to imagine how a specimen of this entity could have reached Thunberg prior to 1794. We have seen a few specimens of this entity from South Africa, collected from 1820 onward, and, regardless of the source of the Thunberg specimen, it was clearly introduced early into the Cape Region. The African specimens we have seen are as follows:

SOUTH AFRICA. CAPE PROVINCE: Near small brooks on the plains near Rondebosch and Wynberg, March 1820, *Ecklon & Zeyher 1762* (SAM). In wet shaded places at Rondebosch and Nieuwland, Feb. 1820, *Ecklon & Zeyher* (SAM). Rondebosch, *Ecklon & Zeyher* (BREM). Along the roads near Newlands, March 1820, *Ecklon & Zeyher* (SAM). Liesbeck River, below Fernwood, Feb. 1944, *Salter* 8895 (BOL, NBG). Lower slopes north of Window Stream, cleared of pines in 1934, Kirstenbosch, April 1946, *Esterhuysen* (PRE).

This species is known as an adventive in Austria, Czechoslovakia, France, Germany, Hungary, and Poland (Raven, 1968: 307), and it may well be that the populations collected in South Africa in the 1940s resulted from a 20th Century reintroduction of the species. Harvey (1862: 506) placed *O. villosa* in the synonymy of *O. biennis* and said, ". . . the Cape specimens very hairy. . . . In Thunberg's time it had already become so wild as to be even then mistaken for an indigenous species." Thunberg was in South Africa from April 1772 to March 1775, which seems very early for a plant of North American origin to have reached the Cape. At any event, it certainly was established in the Cape by 1820, despite the seeming unlikelihood of such an event. There seems to be no reason to doubt the authenticity of the specimen preserved in the Thunberg herbarium, and the name *Oenothera villosa* Thunb. must therefore be taken up for the species generally known as *O. strigosa*. That name is in any case preoccupied by *O. depressa* Greene (1891), as shown by the following partial synonymy (see Munz, 1965: 136, for a more complete version):

Oenothera villosa Thunb., Prodr. Fl. Cap. 75. 1792.
Oenothera villosa subsp. **villosa.**

Oenothera depressa Greene, Pittonia 2: 216. 1891. TYPE: Cultivated at Berkeley, Calif., the seeds from near Custer, Yellowstone Co., Montana, sent by Mr. Blankinship, 1891, *E. L. Greene* (UC).

Oenothera canovirens Steele, Contr. U.S. Natl. Herb. 13: 365. 1911. TYPE: Illinois, Morgan Co., ca. 2 mi S of Concord, 20 Aug. 1910, *E. S. Steele* (US-618797).

Oenothera hungarica Borbás, Kert 1902: 204. 1902; Magyar Bot. Lap. 2: 247. 1903. TYPE: Naturalized in Hungary.
Oenothera strigosa (Rydb.) Mack. & Bush subsp. *canovirens* (Steele) Munz, N. Amer. Fl., ser. 2, 5: 136. 1965.

Oenothera villosa subsp. **strigosa** (Rydb.) Dietrich & Raven, comb. nov.

Based on *Onagra strigosa* Rybd., Mem. New York Bot. Gard. 1: 278. 1900. LECTOTYPE: Montana, Madison Co., Pony, 8 and 12 July 1897, *P. A. Rydberg & E. A. Bessey* (NY); Munz, N. Am. Fl., ser. 2, 5: 136. 1965.
Oenothera strigosa (Rydb.) Mack. & Bush, Fl. Jackson Co., Missouri 139. 1902.

Oenothera villosa subsp. **cheradophila** (Bartlett) Dietrich & Raven, comb. nov.

Based on *Oenothera cheradophila* Bartlett, Bot. Gaz. (Crawfordsville) 44: 302. 1904. TYPE: Washington, Klickitat Co., Bingen, low sandy river bank, 20 August 1906, *W. N. Suksdorf 5860* (GH).
Oenothera strigosa (Rydb.) Mack. & Bush var. *cheradophila* Gates, Rhodora 59: 15. 1957.
Oenothera strigosa (Rydb.) Mack. & Bush subsp. *cheradophila* (Bartlett) Munz, N. Amer. Fl., ser. 2, 5: 136. 1965.

This work was supported by a series of grants from the U.S. National Science Foundation.

LITERATURE CITED

HARVEY, W. H. 1862. Onagrarieae. *In* W. H. Harvey & O. W. Sonder, Flora Capensis. Vol. 2: 503–506. A. S. Robertson, Cape Town, South Africa.
JUEL, H. O. 1918. Plantae Thunbergianae. Almquist & Wiksells, Uppsala, Sweden.
MUNZ, P. A. 1935. Studies in Onagraceae. IX. The subgenus *Raimannia*. Amer. J. Bot. 22: 645–663.
———. 1965. Onagraceae. N. Amer. Fl., ser. 2, 5: 1–278.
RAVEN, P. H. 1968. *Oenothera*. *In* T. G. Tutin et al. (editors), Flora Europaea. Vol. 2: 306–308. University Press, Cambridge.

—*Werner Dietrich, Botanisches Institut der Universität Düsseldorf, D-4000 Düsseldorf 1, Germany* and *Peter H. Raven, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.*

SPECIFIC STATUS FOR *CAMISSONIA CLAVIFORMIS* SUBSP. *WIGGINSII* (ONAGRACEAE)

Of the 11 subspecies of the highly polymorphic *Camissonia claviformis* (Torr. & Frém.) Raven recognized in my revision of the genus (Raven, 1969), one, subsp. *wigginsii* (Raven) Raven, is endemic to Mexico. All ten other subspecies, which occur from southeastern Oregon and adjacent Idaho to northeastern Baja California, Arizona, and northwestern Sonora, are genetically self-incompatible, with the stigma held well above the anthers at anthesis. Judged from the very few available herbarium specimens, the same was thought to be true of subsp. *wigginsii*: the stigma apparently was elevated above the anthers, and despite the appearance of the flowers, which are much smaller than in any of the other subspecies, it was earlier judged to be outcrossing also (Raven, 1969: 221).

On 27 March 1972, I had the opportunity to study a small population of this taxon, growing with *Camissonia cardiophylla* (Torr.) Raven subsp. *cedrosensis* (Greene) Raven on the sandy floor of the Arroyo de Calamajué ca. 70 km south

of Bahía San Luis Gonzaga (*Raven 26061*, MO), in a plant community dominated by *Prosopis*, with *Washingtonia* and *Juncus* frequent along the wash. In these living plants, it was evident that the flowers were highly autogamous, the anthers being appressed directly to the stigma at anthesis. In view of this important biological discontinuity between them and the other elements grouped as *Camissonia claviformis*, the following new combination becomes appropriate:

Camissonia wigginsii (Raven) Raven, stat. nov.

Based on *Oenothera clavaeformis* Torr. & Frém. subsp. *wigginsii* Raven, Univ. Calif. Publ. Bot. 34: 103. 1962.

Camissonia claviformis (Torr. & Frém.) Raven subsp. *wigginsii* (Raven) Raven, Brittonia 16: 282. 1964.

Dr. William Tai examined fixed material of *Raven 26061*, and found 7 bivalents at diakinesis. This is in agreement with my earlier report of the chromosome number of the taxon (Raven, 1969: 221).

Camissonia wigginsii has yellow petals 1.5–2 mm long, filaments 1.5–2 mm long, and a style 5–7 mm long, whereas *C. claviformis* has white or yellow petals 2.5–8 mm long, filaments 2–5.5 mm long, and a style 7–16 mm long. As mentioned above, the stigma is elevated above the anthers in all ten subspecies of *C. claviformis*, and they are uniformly genetically self-incompatible. In contrast, the anthers surround and shed pollen directly on the stigma in *C. wigginsii*, which is therefore highly autogamous. *Camissonia wigginsii* seems to have been derived from populations of *C. claviformis* similar to those that are closest geographically and most similar morphologically, namely *C. claviformis* subsp. *peirsonii* (Munz) Raven and *C. claviformis* subsp. *rubescens* (Raven) Raven. The derivative *C. wigginsii*, a local endemic of central Baja California from 150–600 m elevation, is separated from the nearest populations of its presumed ancestral species by a gap of some 120 km. Thus the relationship between *C. wigginsii* and *C. claviformis* is similar to that between *Oenothera brandegeei* (Munz) Raven, a rare autogamous annual species of central Baja California, and *O. caespitosa* Nutt., a polymorphic self-incompatible perennial of the southwestern United States from which it has undoubtedly been derived (Raven, 1970). In both genera, the autogamous derivative taxa in central Baja California probably have evolved in relation to spreading aridity in the late Pleistocene or subsequently.

Support from the U.S. National Science Foundation is gratefully acknowledged. I am grateful to Dr. William Tai of Michigan State University for the chromosome count reported here.

LITERATURE CITED

RAVEN, P. H. 1969. A revision of the genus *Camissonia* (Onagraceae). Contr. U.S. Natl. Herb. 37: 161–396.

———. 1970. *Oenothera brandegeei* from Baja California, Mexico, and a review of subgenus *Pachylophus* (Onagraceae). Madroño 20: 350–353.

—Peter H. Raven, Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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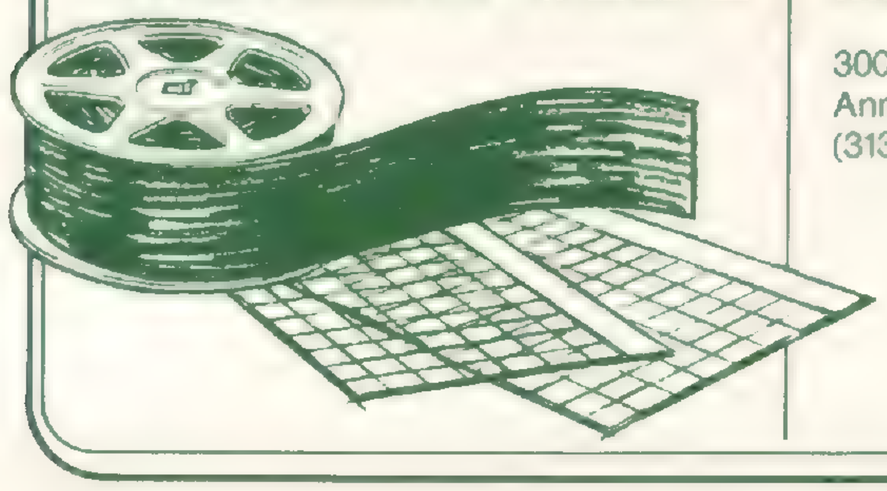

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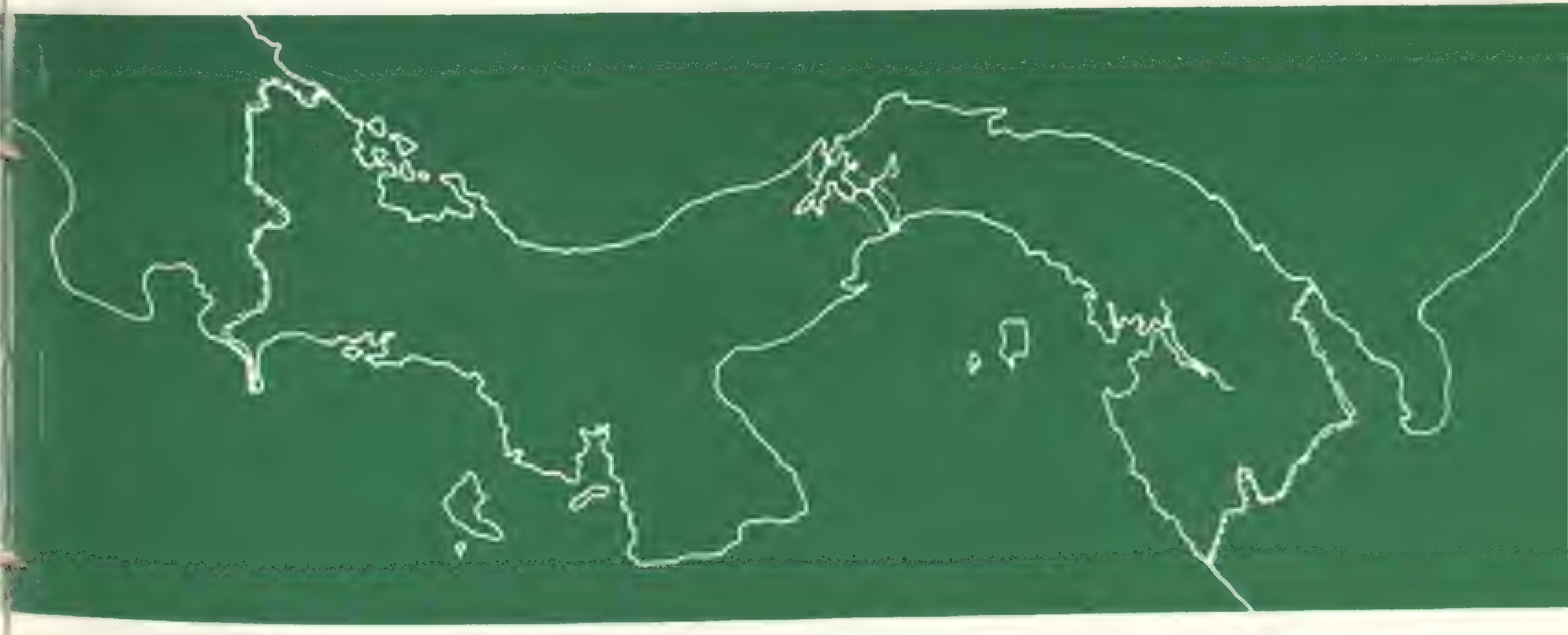

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ANNALS
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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IV

FAMILY 55. BATACEAE

W. G. D'ARCY[2]

Monoecious or dioecious *shrubs*; branching opposite or alternate. *Leaves* borne on short shoots, opposite, simple, succulent, linear, with pointed apices and drying with umbonate or appendaged bases; stipules minute, caducous. *Inflorescences* axillary or terminal, in monoecious species the flowers solitary or in clusters on short, leafy axes, in dioecious species congested in short catkins. Male *flowers* subtended by a single bract and by a pair of tepallike bracteoles (spathella), the stamens 4, alternating with minute staminodes or appendages, the anthers exserted, dorsifixed, versatile, introse, dehiscing longitudinally, 2-locular; female flowers free or fused into a syncarp, 2-carpellate but 4-locular by a false septum, the ovule 1 in each locule, bitegmic, crassinucellate, erect, basal, epitropous, anatropous, the raphe facing the carpel axis, the style wanting or short, the stigmas 2, fimbriate, persistent. *Fruits* syncarps or drupes, the outer tissues fleshy or leathery, the endocarp woody, each pistil with 1–4 seeds; seeds oblong, nearly straight, the embryo nearly straight, the endosperm wanting.

Although intensively investigated by several workers, e.g., McLaughlin, 1959; van Royen, 1956; Uphof, 1930; and van Heel, 1958, there is still disagreement on several important features of these plants, e.g., whether the ovary is superior or inferior and the nature of the perianth and fruit. In the past it has been placed in alliance with a considerable variety of families, but the practice

[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 63: 385–388. 1976.

in recent years of placing it in conjunction with the Centrospermae has been discredited (Goldblatt, 1976).

Literature:

Goldblatt, P. 1976. Chromosome number and its significance in *Batis maritima* (Bataceae). J. Arnold Arbor. 57: in press.
Heel, W. A. van. 1958. Additional investigations on *Batis argillicola.* Nova Guinea, n.s., 9: 1–7.
Johnson, D. S. 1935. The development of the shoot, male flower and seedling of *Batis maritima* L. Bull. Torrey Bot. Club 62: 19–31.
McLaughlin, J. 1959. The woods and flora of the Florida Keys: wood anatomy and phylogeny of Batidaceae. Trop. Woods 110: 1–15.
Royen, P. van. 1956. A new Batidaceae, *Batis argillicola.* Nova Guinea, n.s., 7: 175–195.
Uphof, J. C. T. 1930. Biologische Beobachtungen an *Batis maritima* L. Oesterr. Bot. Z. 79: 355–367.

1. BATIS

Batis P. Browne, Civ. Nat. Hist. Jam. 356. 1756. TYPE: *B. maritima* L.

Glabrous, monoecious or dioecious *shrubs*, often nodding or prostrate; the bark flaking off; branching alternate, sometimes rooting and branching at the nodes. *Leaves* opposite, succulent, linear, apically pointed or mucronate, basally clasping but drying with an umbonate appendage; stipules inconspicuous, caducous. *Inflorescences* axillary or terminal, in monoecious species the flowers borne separately on short leafy axes (brachyblasts) with male and female flowers sessile on the same shoot, in dioecious species the flowers borne in short, dense axillary catkins or syncarps. Male *flowers* subtended by a bract or leaf and surrounded by a pair of tepallike bracts (spathella), the stamens 4, alternating with 4 staminodes or appendages, the anthers ovoid, exserted, the filaments glabrous, the gynoecium rudimentary or wanting; female flowers or catkins subtended by a pair of scalelike bracts or by leaves, the pistils fused or separate, when fused bearing a scalelike bract near the apex, the pistil 4-locular, each locule with a single erect, basal ovule, the style persistent, short or wanting, the stigmas 2-capitate, fimbriate, persistent. *Fruits* drupes or syncarps, the outer tissues fleshy or leathery, the endocarp woody; seeds 1–4 in each pistil, oblong, nearly straight.

This genus includes two contrasting species, one *B. maritima*, common along seacoasts of the New World with outlying populations in the Hawaiian Islands and Galapagos Islands, and the other, *B. argillicola* van Royen, restricted to the south coast of New Guinea. The American species is a prostrate, dioecious shrub which grows on sea flats and under mangroves, usually in intimate contact with the sea, whereas the New Guinea species is an erect shrub with monoecious flowers growing on silty clay pans at seaside. In the American species, the flowers are united in short, conelike catkins whereas in the New Guinea species they are separate or free in small clusters on short shoots, each flower or cluster subtended

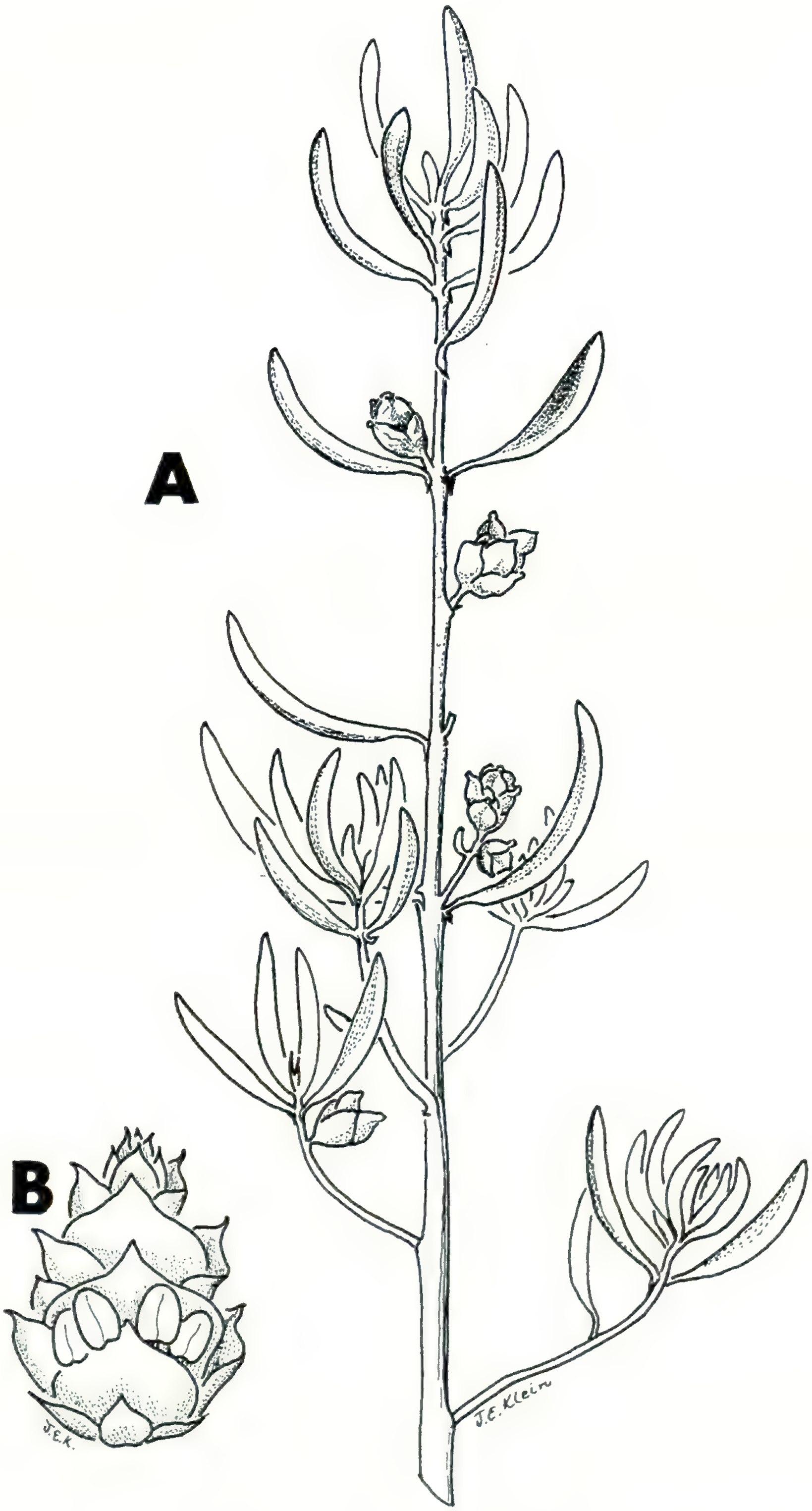

FIGURE 1. *Batis maritima* L.—A. Habit of pistillate plant (×1). [After *Spellman & Stoddart 2232* (MO), Belize.]—B. Staminate inflorescence (×6). [After *Palmer 326* (MO), Mexico.]

by a leaf. The occurrence of this genus along seacoasts suggests dispersal by ocean currents, but this raises the question of why the genus is not more widespread in the Old World. Johnson (1935) commented that seedlings are almost never found in nature.

1. **Batis maritima** L., Syst. Nat., ed. 1. 289. 1759. TYPE: not seen.—FIG. 1.

Prostrate, glabrous, dioecious *shrubs*, the bark soon flaking off; rooting at the nodes, the branching alternate, the leafy short shoots with elevated, faintly 2-lobed leaf scars and immediately above them minute bud scars. *Leaves* succulent, linear, terete or approximately 3–4-angled in cross-section, to 2 cm long, apically acute or mucronate, basally clasping and drying with a basal, reflexed appendage; stipules inconspicuous, caducous. *Inflorescences* axillary, shortly pedunculate, congested, indeterminate catkins or syncarps subtended by an opposite pair of scalelike bracts, not enlarging or enlongating much with age. Male inflorescence with 10–30 pairs of decussate *flowers*, each surrounded by a campanulate, 2-lobed perianth which is appendaged on the dorsal side just below the rim to give the appearance of imbricate bracts, the flower consisting of 4 stamens alternating with 4 minute spatulate, petaloid staminodes, the anthers ovoid, dorsifixed, versatile, introrse, dehiscing longitudinally, exserted on stout, glabrous filaments, the gynoecium wanting; female inflorescence an irregularly ellipsoidal syncarp to 5 mm long of 4–8 fused pistils which bear persistent, scalelike, 1 mm wide tepals near their apices, the style umbonate, the 2 stigmas capitate and connivent, the ovary with 4 unequal locules and one basal ovule in each locule. *Fruits* drupaceous syncarps with 1–several pyrenes, the outer tissue fleshy or leathery, the endocarp woody; seeds oblong, nearly straight.

Batis maritima may be recognized by its succulent, almost rubbery leaves held upright on prostrate, naked, woody stems, and by its flowers and fruits which are in small, axillary, conelike inflorescences.

Although widespread and common along coastlines in the Caribbean and tropical Pacific, *Batis maritima* has been recorded only once from Panama. In other countries it is frequently met in flat, tidal marshes and under black mangroves (*Avicennia germinans*), sometimes covering large areas. This species builds up considerable quantities of salt in its tissues and the leaves have a strong, salty taste.

Common names include "samphire," "saltwort," "barilla" (Puerto Rico).

PANAMA: E side of Punta Chame, *D'Arcy 10211* (MO, PMA).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part V

FAMILY 76A. DROSERACEAE[2]

M. D. CORREA A.[3] AND A. S. TAYLOR B.[3]

Low *herbs*, often stemless. *Leaves* alternate, mostly basal, in rosettes, often circinate in bud, with glandular hairs and sticky secretion which trap small insects; stipules present or absent. *Inflorescences* usually circinate cymes or racemes. *Flowers* perfect; sepals 4–8, more or less connate at the base, imbricate, persistent; petals 4–8, hypogynous, imbricate, marcescent; stamens 4–20, the filaments usually free, filiform or nearly so, the anthers 2-locular, extrorse, opening by longitudinal slits; ovary superior, free, 2–5-carpellate, with 1 locule, the placenta parietal or subbasal, the ovules numerous, anatropous, the styles 3–5, usually free, simple or divided. *Fruits* usually loculicidally dehiscent; seeds minute, dark colored, variously reticulate and ornamented.

1. DROSERA

Drosera L., Sp. Pl. 281. 1753; Gen. Pl. 136. 1754. TYPE: *D. rotundifolia* L.

Rossolis Adanson, Fam. Pl. 2: 245. 1763.
Esera Neck., Elem. Bot. 2: 160. 1790.
Dismophyla Raf., Fl. Tell. 3: 36. 1836.
Adenopa Raf., Fl. Tell. 3: 37. 1836.
Filicirna Raf., Fl. Tell. 3: 37. 1836.
Sondera Lehm., Pugill. 8: 44. 1844.

Low insectivorous *herbs*. *Leaves* alternate, usually in basal rosettes, covered with glandular hairs having viscid secretion; blades filiform to broadly orbicular, circinate in bud; stipules scarious, variously fringed or divided, adnate or free. *Inflorescences* circinate, nodding at the underdeveloped apex. *Flowers* regular, hypogynous, generally pentamerous; sepals 4–8, usually 5, withering-persistent, distinct or mostly united at the base, imbricate; petals 4–8, usually 5, white, pink or purple, broadened at the tip, distinct or slightly united at the base; stamens 4–8, as many as the petals, the filaments subulate or filiform, the anthers slightly extrorse and versatile; ovary superior, sessile, 1-celled, many-ovuled, the placentas

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[1] Assisted by National Science Foundation Grant BMS72-02441 A03 (Thomas B. Croat, principal investigator).

[2] We gratefully acknowledge the curators of the following herbaria for the loan of specimens: CR, DUKE, MEXU, MO.

[3] Escuela de Biología, Facultad de Ciencias Naturales y Farmacia, Universidad de Panamá, Estafeta Universitaria, Panamá, Panamá.

ANN. MISSOURI BOT. GARD. 63: 389–392. 1976.

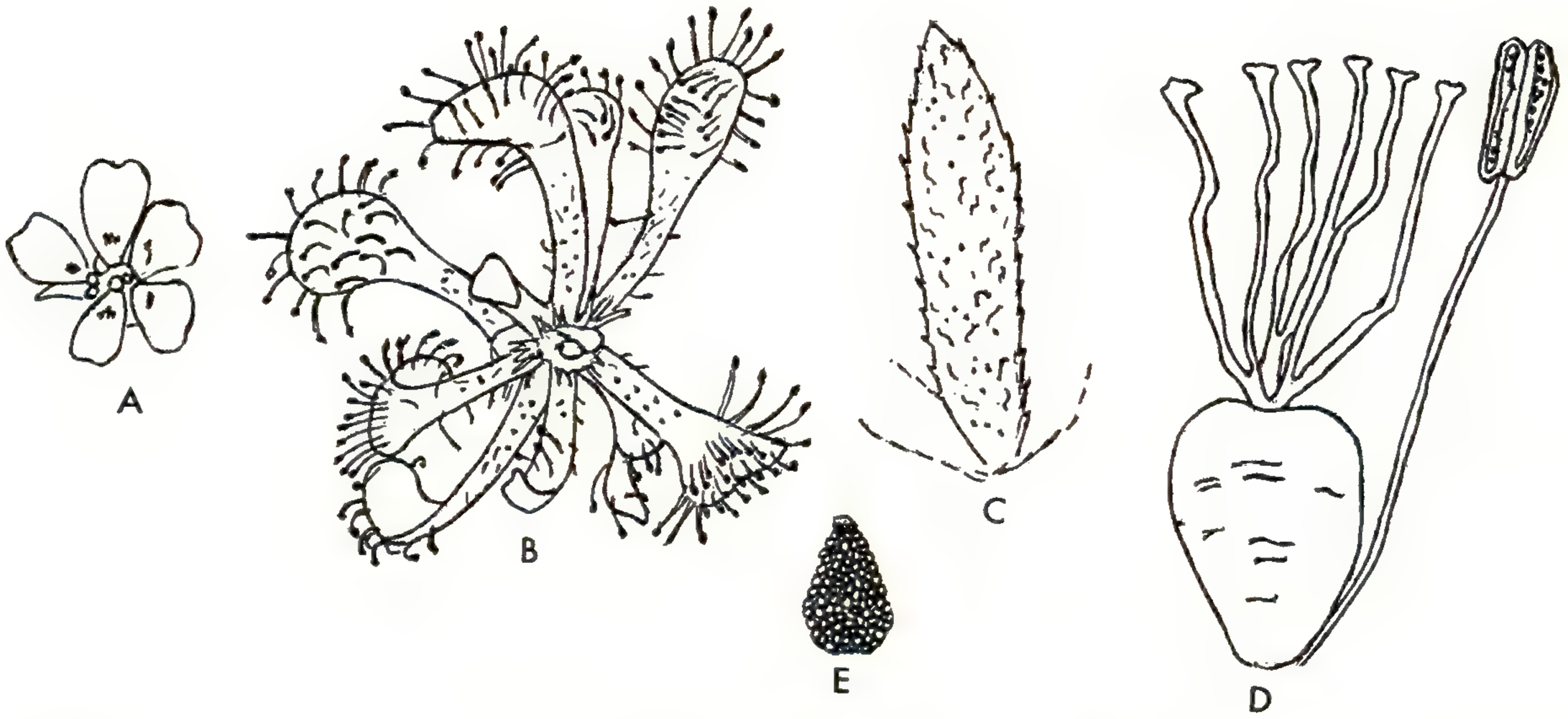

FIGURE 1. *Drosera panamensis* M. D. Correa & A. S. Taylor.—A. Flower (×1).—B. Habit (×2½).—C. Sepal (×10).—D. Gynoecium and part of androecium, the perianth removed (×10).—E. Seed (×20). [After *Correa et al. 1949* (PMA).]

3–5, parietal, the ovules subglobose or ovoid in 2–5 rows on each placenta, anatropous, the styles 2–5, usually 3, often bifurcate to the base or branched. *Capsules* 2–5-valved, usually 3-valved; seeds minute, numerous, usually stipitate, the testa variously reticulated and ornamented.

The genus is cosmopolitan with 100 tropical and temperate species, many in Australia and New Zealand.

1. **Drosera panamensis** M. D. Correa & A. S. Taylor.[4] TYPE: Panama, *Correa et al. 2215* (PMA, holotype; CHR, COL, DUKE, F, K, MEXU, MO, NSW, U, US, isotypes).—Fig. 1.

Annual, small insectivorous *herbs*. *Leaves* subopposite, 13–15 mm long, in basal rosettes, little distinction between blade and petiole, covered with elongate red-greenish trichomes having small oblong glandular heads; blades broadly spatulate to obovate-orbicular, 6–8 mm long, 3.5–5 mm wide; stipules adnate-

[4] *Drosera panamensis* M. D. Correa & A. S. Taylor, sp. nov. Herbulae annuae insectivorae subopppositifoliae. Folia 13–15 mm longa, lamina late spathulatae ad obovati-orbicularem, 6–8 mm longa, 3.5–5 mm lata; stipulae adnatae, fimbriatae, 2.5 mm longae. Scapus parce pubescens, glandulosus, teres vel compressus, 9–10 cm longus, ferens flores (1–)2–3(–4) circa ad apicem. Flores calyce sepalorum 5, distinctorum praeter bases; sepala oblongolanceolata parce puberulonga glandibus pusillis sessilibus in pagina externa, margo spinulosus, acutus, 5–6 mm longus, 1.5 mm latus; petala 5, dimorpha, grandiora 3, parviora 2, marcida, oblongolanceolata ad obovata, obtusa, plerumque emarginata, 8 mm longa, 1.5 mm lata, unguis 4 mm longus; stamina 5, libera, 5.5–6 mm longa, filamenta complanata, antherae basifixae, placenta 3, styli 3, bifurcati fere ad basem, 3 mm longi, stigmata apparenter decursiva et expansa ad apicem stylum in ½–⅓ partem distale tagentia. Capsula obovoidea, rugosa, 3–4 mm longa, 2 mm lata; semina nigra, minuta, oblongo-ovata, aliqui leviter plana ad apicem, grosse crateriforma, 0.3–0.4 mm longa.

Species nova in habitum proxima *D. brevifolia* Pursh et *D. leucantha* Shinners sed in typum trichomatis, formam et magnitudem sepalorum et petalorum, margines spinulosos sepalorum differt.

fimbriate, 2.5 mm long. *Scape* sparingly pubescent, glandular, terete or slightly compressed, 9–10 cm long, bearing (1–)2–3(–4) flowers toward the last 2 cm, pilose. *Flowers* with the calyx of 5 sepals, distinct but united toward the base; sepals oblong-lanceolate, sparingly pubescent with very minute sessile glands on the outer surface, the margin spinulose, acute, 5–6 mm long, 1.5 mm wide; petals 5, dimorphic, free, 3 larger, 2 smaller, marcescent, oblong-lanceolate to obovate, obtuse, mostly emarginate, 8 mm long, 1.5 mm wide, the claw 4 mm long; stamens 5, free, 5.5–6 mm long, the filament complanate, the anthers basifixed; ovary superior, 3-carpellate, 1-loculed with many ovules in the locule, the 3 placentas parietal, the styles 3, bifurcate almost to the base, 3 mm long, the stigmas apparently decurrent and expanded at the apex and the distal ½–⅓ of the style. *Capsules* obovoid, rugose, 3–4 mm long, 2 mm wide; seeds black, minute, oblong-ovate, some slightly flat at the top (distally), coarsely crateriform, 0.3–0.4 mm long.

Drosera panamensis grows in poor soils in open places at high elevations. The flowering period is short, from June to July. In the greenhouse, flowers fade in about 24 hours following anthesis and whole plants have changed in color from reddish to complete green, but the reason for this is unknown.

VERAGUAS: La Yeguada, road between Altos de la Gallota and Cerro Verde, 1000 m, *Correa et al. 1949* (PMA). La Yeguada, Altos de Baltazar y el Veladero, 650 m, *Correa et al. 2215* (CHR, COL, DUKE, F, K, MEXU, MO, NSW, PMA, U, US). Close to La Laguna La Yeguada, 600 m, *Vergara 130* (DUKE, MO, PMA).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 105. STAPHYLEACEAE

THOMAS B. CROAT[2]

Trees or *shrubs*. *Leaves* opposite or alternate, petiolate; blades simple or pinnately compound; leaflets serrate; venation pinnate; stipules and stipels usually present, sometimes reduced to glands or absent. *Inflorescences* terminal or in the axils of the upper leaves, paniculate or thyrsiform. *Flowers* complete, bisexual and actinomorphic; sepals 5, free, unequal, imbricate; petals 5, free, unequal, imbricate in bud, inserted on or below a hypogynous crenate or lobed disc; stamens 5, arising between the lobes of the disc, alternate with the petals, the filaments complanate, the anthers 2-celled, dehiscing longitudinally; ovary superior, entire or lobed or 3-parted, 3-locular, the carpels free or united, sessile, the placentation axile, the ovules few to many, anatropous, in 1 or 2 series on the ventral suture, the styles 3, free or united, the stigmas capitate. *Fruit* a berry (Panama) or a membranous inflated capsule dehiscing apically; seeds with a straight embryo and fleshy endosperm.

The Staphyleaceae includes 5–7 genera and about 60 species, mostly from North America. The genus *Staphylea* is principally temperate but reaches Mexico. *Staphylea* and *Turpinia* have species occurring in both Asia and the Americas. The genus *Hertia* occurs in the West Indies and in South America. The remaining genera are of the Old World.

Literature:

Spongberg, S. 1971. Staphyleaceae in the Southeastern United States. J. Arnold Arbor. 52: 196–203.

1. TURPINIA

Turpinia Vent., Choix Pl. *tab. 31.* 1803, nom. cons. TYPE: *T. paniculata* Vent.

Dalrympelea Robx., Hort. Beng. 17. 1814. TYPE: *D. pomifera* Robx. = *Turpinia pomifera* (Roxb.) DC.

Eyrea Champ. ex Benth., Hooker's J. Bot. Kew Gard. Misc. 3: 331. 1851. TYPE: *E. vernalis* Champ. ex Benth. = *Turpinia arguta* (Lindl.) Seem.

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[1] Assisted by National Science Foundation Grant BMS72-02441 A03 (Thomas B. Croat, principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

Lacepedea H.B.K., Nov. Gen. Sp. Pl. 5: 142, *tab. 144.* 1821. TYPE: *L. insignis* H.B.K. = *Turpinia insignis* (H.B.K.) Tulasne.
Ochranthe Lindl., Bot. Reg. *tab. 1819.* 1836. TYPE: *O. arguta* Lindl. = *Turpinia arguta* (Lindl.) Seem.
Triceraia Willd. ex Roem. & Schult., Syst. Veg. 4: 803. 1819. TYPE: *T. tinifolia* Roem. & Schult. = *Turpinia insignis* (H.B.K.) Tulasne.

Trees or *shrubs. Leaves* opposite, petiolate; blades simple or pinnately compound; leaflets serrate; venation pinnate; stipules and stipels usually present. *Inflorescences* terminal or in the axils of the upper leaves, paniculate or thyrsiform. *Flowers* complete, bisexual and actinomorphic; sepals 5, free, unequal, imbricate; petals 5, free, unequal, imbricate in bud, inserted on or below a hypogynous crenate or lobed disc; stamens 5, arising between the lobes of the disc, alternate with the petals, the filaments complanate, the anthers 2-celled, dehiscing longitudinally; ovary superior, entire or lobed, 3-locular, 3-carpellate, sessile, the placentation axile, the ovules few, anatropous, the styles 3, free or united, the stigmas capitate. *Fruit* a berry; seeds with straight embryo and fleshy endosperm.

Turpinia is a genus with probably fewer than 10 species. A single variable species occurs in Panama, and 2 or 3 other taxa occur also in Central America, though all may be only subspecifically distinct.

aa. Flowers less than 3.5 mm long; pedicels glabrous or very weakly puberulent; fruits rounded at the apex; leaf blades glabrous on the midrib of the lower surface; growing at elevations from near sea level to ca. 850 m ..... 1b. *T. occidentalis* subsp. *breviflora*
a. Flowers more than 3.5 mm long when fully expanded; pedicels usually conspicuously puberulent to villous; fruits bearing 3 conspicuous horny projections at the apex; leaf blades usually puberulent or villous along the midrib of the lower surface; usually growing at elevations from 1,000 to 3,200 m ..... 1a. *T. occidentalis* subsp. *occidentalis*

1. **Turpinia occidentalis** (Swartz) G. Don, Hist. Dichl. Pl. 2: 3. 1832.

1a. **Turpinia occidentalis** subsp. **occidentalis**

Staphylea occidentalis Swartz, Prodr. Veg. Ind. Occ. 55. 1788. TYPE: Jamaica (not seen).
S. *heterophylla* Ruiz & Pavón, Fl. Peruv. Chil. 3: 29, *tab. 253.* 1802. TYPE: Peru, ad Mespata et Muna, *Ruiz & Pavón* (F, fragment).
Turpinia paniculata Vent., Choix Pl. *tab. 31.* 1803. TYPE: Santo Domingo, *Poiteau & Turpin* (not seen).
Lacepedea pinnata Schiede, Linnaea 10: 240. 1836. TYPE: Mexico, Vera Cruz, between Acatlán and Chiconquico, *Schiede 309* (MO).
Turpinia heterophylla (Ruiz & Pavón) Tulasne, Ann. Sci. Nat. Bot., sér. 3, 6: 363. 1846.
T. schiedeana Tulasne, Ann. Sci. Nat. sér. 3, 7: 296. 1847, based on *Lacepedea pinnata* Schiede.
T. pinnata (Schiede) Hemsley, Biol. Centr. Amer., Bot. 1: 216. 1880.
T. glandulosa Bello, Anales Soc. Esp. Hist. Nat. 10: 250. 1881. TYPES: Haiti, in montibus Furcy, 1515 m, *Picarda 790, 833* (not seen).

Trees to 18 m tall and 30 cm d.b.h.; periderm with many, close, small, vertical fissures; inner bark brown with white markings; sap without odor, glabrate throughout. *Leaves* opposite, 3–9-foliolate; petiole 4–6(–11) cm long; petiolules less than 1 cm long, longer on terminal leaflets; leaflets elliptic or ovate-elliptic, acuminate, attenuate to rounded at the base, 6–13 cm long, 2.5–6.5 cm wide, sharply to obscurely serrate-crenate; stipules inconspicuous. *Inflorescences* terminal or upper-axillary, much-branched panicles to 30 cm long; pedicels 1–3 mm

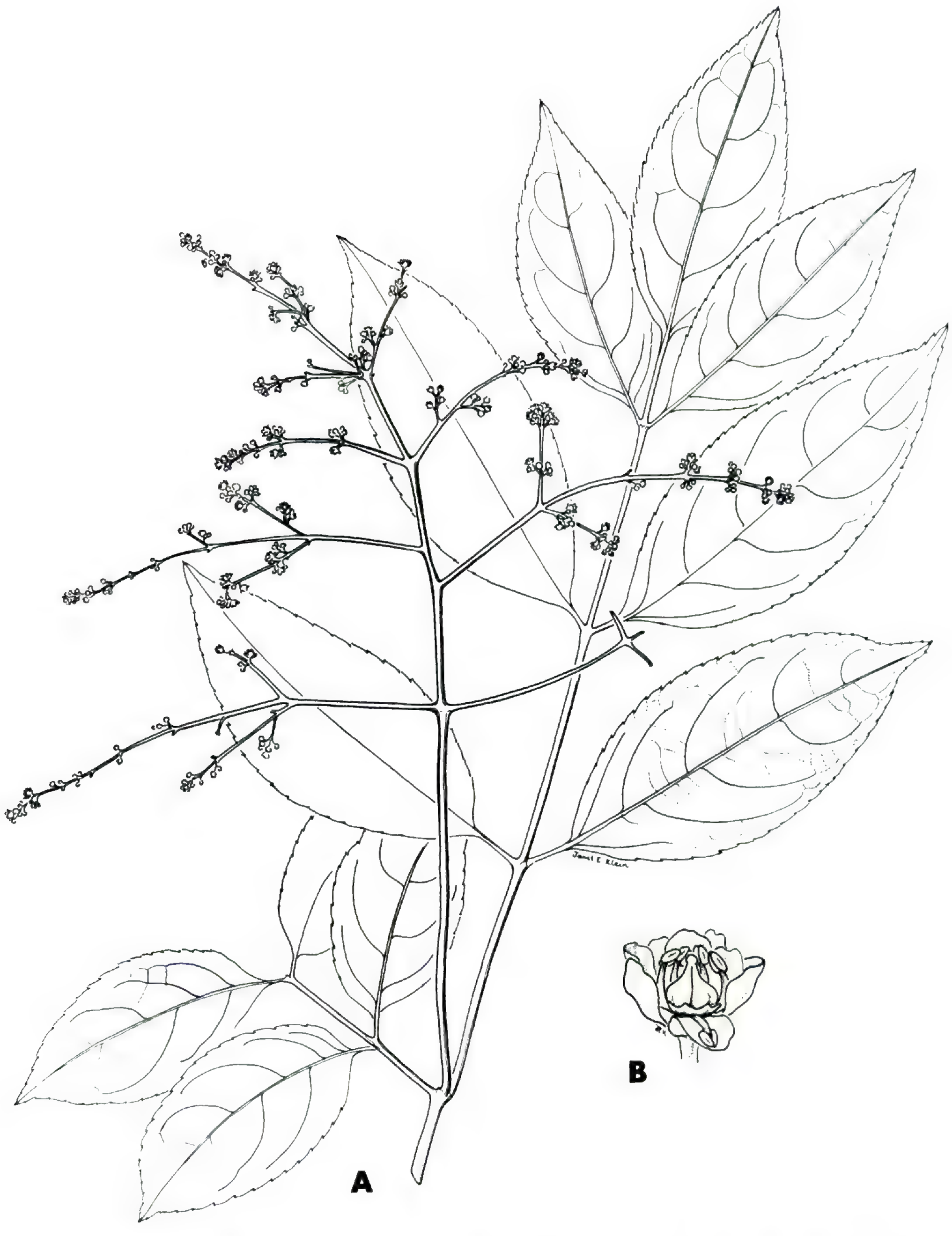

FIGURE 1. *Turpinia occidentalis* subsp. *breviflora* Croat.—A. Flowering branch (×½). —B. Flower (×4½). [After *Croat 4820* (MO).]

long. *Flowers* 5-parted sepals concave, at least one somewhat longer than the others, to 2.7 mm long, rounded at the apex, persisting in fruit; petals white, obovate, rounded at the apex, 2.3–2.7 mm long; stamens 5, as long as the petals, alternating with them from between the lobes of a crenate or lobed disc, the

anthers ovate, attached at the center, the thecae directed upward; pistil of 3 free carpels, the styles connate at anthesis, later becoming free, the stigmas united, held at about the level of the anthers. *Berries* yellow, subglobose to obovate, 3-locular, to 2 cm diam., with 3 radial grooves at the apex; seeds several per locule, irregularly ovate, 4–5 mm long, smooth, orange brown.

Turpinia occidentalis ranges from Mexico and the West Indies to Venezuela, Peru, and Brazil. It flowers from April to June (rarely as late as August) and fruits mature from August to November.

Turpinia occidentalis is quite variable in most aspects including number of leaflets, degree of pubescence, and flower size. There seems to be no evidence that characters used by Ventenat to separate *T. occidentalis* and *T. paniculata* are valid. He separated them on the basis of alternate versus opposite leaves, bisexual versus polygamodioecious flowers, unlobed versus crenate disc, and oblong seeds 1 per locule versus subrounded seeds, more than 1 per locule. Both taxa were described from West Indian material and both are apparently based on large-flowered plants. The species can be divided with some difficulty into at least two subspecies. The typical subspecies has larger flowers and larger fruits which are often at least weakly tricornate. It also generally inhabits regions above 1,000 m elevation. The smaller-flowered subspecies, long going by the name *T. paniculata* Vent., is newly named here since Ventenat's plate clearly shows the large-flowered plant. The small-flowered subspecies, occurring principally in the lower part of Central America and at lower elevations, is mostly replaced by the typical subspecies in western, upland Panama as well as elsewhere in middle America and Mexico.

Perhaps also worthy of recognition as subspecies are two other forms. One of these is represented by *Allen 4741* and *Stern et al. 2043*, both from Chiriquí Province at elevations above 1,500 m. This form differs from the typical variety in having leaflets remotely crenate-serrate with more prominent reticulate venation.

The second form differs from the typical subspecies in having smaller leaflets which are closely serrate and dry dark. Flowering is somewhat precocious and leaves on flowering plants may be not fully developed. Examples of this form are: *Kirkbride & Duke 855, 941*; *Croat 26412*; *Mori & Kallunki 5892*; *Gentry 2042*; *Davidson 375, 456*. Both forms are cited below with the typical subspecies.

CHIRIQUÍ: Finca Lérida, slopes of Quebrada Velo, 5000 ft, *Allen 4741* (MO). Las Nubes, ca. 2000 m, *Croat 26412* (CAS, DUKE, F, GH, MO, PMA, TEX). Above Boquete on road to Cerro Horquete, 1400–1600 m, *Croat 27033* (MICH, MO, P, PMA). Bajo Chorro, vic. Boquete, 6000 ft, *Davidson 375, 456* (both F, MO). Cerro Horqueta, ca. 1500 m, *Duke et al. 13662* (DUKE). Boquete, Cerro Horqueta, 5000–6000 ft, *Dwyer & Hayden 7716* (CAS, DAV, MISSA, MO, PMA, VEN). Cerro Respinga, along Boquete Trail, 2000–2500 m, *Gentry 5941* (MO, PMA, RSA, VEN). Between Pinola and divide on Chiriquicito-Caldera Trail, *Kirkbride & Duke 855* (MO). Between Quebrada Hondo and divide on Caldera-Chiriquicito Trail, *Kirkbride & Duke 941* (MO). Boquete, 4500 ft, *Lao 375* (MO). Cerro Colorado, 50 km N of San Félix, 1200–1500 ft, *Mori & Dressler 7799* (MO, NY, PMA). North of San Félix at Chiriquí-Bocas del Toro border, 5000–5500 ft, *Mori & Kallunki 5892* (F, MO, PMA, US). Boquete, Finca Collins, 5800–6700 ft, *Stern et al. 33795* (MO). Cerro Punta, ca. 6000 ft, *Tyson 7028* (PMA). VERAGUAS: Cerro Tute ca. 10 km NW of Santa Fé, *Mori 6280* (F, MO, PMA).

1b. **Turpinia occidentalis** subsp. **breviflora** Croat.[3] TYPE: Panama, Canal Zone, *Croat 10874* (MO-2038838, holotype; DUKE, NY, isotypes).—FIG. 1.

Trees to 18 m tall. *Leaves* opposite, 3–9-foliolate, the lower midrib and blade surface glabrous. *Inflorescence* branches and pedicels glabrous to minutely and sparsely puberulous. *Flowers* white, less than 3 mm long; petals 2.3–2.7 mm long; stamens as long as the petals; ovary ovoid, gradually to abruptly narrowed to the style, the style and ovary together equalling the petals, the stigma held at the level of the anthers. *Fruits* rounded at the apex, lacking any conspicuous enlarged style branches.

This taxon is similar to the typical variety except for its smaller flowers, glabrous leaflets, and rounded fruits.

Subspecies *breviflora* ranges from Mexico to Colombia and the West Indies. It is most abundant in lower middle America and Panama at elevations from sea level to 850 m. Its flowering and fruiting behavior is the same as the typical subspecies.

CANAL ZONE: Barro Colorado Island, *Bangham 592* (A, F, US); *Croat 4820* (MO), *10874* (DUKE, MO, NY), *15048* (F, GH, MO, NY), *17048* (GH, MO, NY); *Dwyer 1422* (F, NY); *Foster 997* (DUKE, F, GH, MO), *1233* (DUKE, F, MO); *Kenoyer 678* (US); *Salvoza s.n.* (A); *Shattuck 1019* (F, MO, US); *Zetek 3559* (F, MO), *3659* (F, MO, US). Pipeline Road, *Lao et al. 14* (F, MO, NY). Around Gamboa, 20–100 m, *Pittier 6648* (GH, NY, US). COCLÉ: El Valle de Antón, 600 m, *Lao 290* (MO). Hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1689* (MO, OS). 3 km NE of El Valle, *Mori & Kallunki 2982* (MO). DARIÉN: Near Tucutí, *Duke 5240* (MO). Río Balsa, between Río Manené and Río Tusijuanda, *Duke 13574* (MO). Vic. of Paya, Río Paya, *Stern et al. 232* (GH, MO, US). Trail from Paya to Pucro, *Stern et al. 415* (GH, MO, US). Shores of Bahia de Piñas, *Stern & Chambers 190* (A, F, MO, NY, US). PANAMÁ: Cerro Campana, 2700–3000 ft, *Duke 8637* (MO, OS, US). VERAGUAS: Above Santa Fé on slopes of Cerro Tute, 3600–4200 ft, *Gentry 6265* (MO).

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[3] *Turpinia occidentalis* (Swartz) G. Don subsp. *breviflora* Croat, subsp. nov. Differt a subspecie typica costa laminaque infra folium glabra, ramis inflorescentae et pedicellis glabris aut puberulis minute sparsimque, floribus minus quam 3 mm longis, petalis 2.3–2.7 mm longis.

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 106. ICACINACEAE[2]

R. A. HOWARD[3]

Trees, *shrubs* or *lianas*, occasionally dioecious. *Leaves* alternate, petiolate, exstipulate, simple, coriaceous or rarely membranous, entire or rarely sinuate-dentate, the veins arcuate and weakly anastomosing. *Inflorescences* cymose or paniculate with cymose branches, terminal, axillary, extra-axillary or supra-axillary, bracteate. *Flowers* articulated below the calyx, perfect, polygamous or unisexual by abortion, hypogynous; calyx small, fleshy, the 5 lobes or teeth, imbricate; petals 5, rarely 4, free or united at the base, valvate, the apex inflexed, fleshy; stamens 5, alternate with the petals, erect, the filaments fleshy, often hairy below the anther, the anthers attached basally or dorsally near the base, with 4, rarely 2 anther sacs, often deeply lobed, dehiscence introrse or lateral, longitudinal; ovary 1-celled, the ovarian appendage or basal disc present or absent, the ovules 2, anatropous, pendant from near the apex, collateral or rarely superposed, the functional style 1, additional rudiments often present, the stigma capitate. *Fruits* drupaceous, symmetrical or flattened, 1-celled, the funicle vascular supply in a special tubular canal of the endocarp or protruding in the locule; seed 1, the embryo minute or large, the endosperm generally copious.

This is a family of 60 genera, 12 occurring in the American tropics in the Greater Antilles, Mexico, Central America, and throughout South America to northern Argentina, generally at lower elevations. It is generally distributed in tropical Africa, India, Malaysia, China, the Philippines, Australia, New Zealand, and Polynesia. The family is not common and is poorly represented in herbaria. Field observations, including floral biology, are almost completely lacking.

The family is most easily recognized by the alternate, exstipulate leaves, the axillary inflorescences, the flowers conspicuously articulated below the calyx, the imbricate calyx lobes (when developed), the valvate petals commonly with inflexed narrow apices, the pistil with a single locule with two apical collateral or superposed ovules of which one develops in a drupaceous fruit.

The genera of the Icacinaceae were at one time considered with those of the

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[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] The author acknowledges with gratitude the courtesy of the directors and curators of the herbaria cited in making valuable material available for this study.

[3] The Arnold Arboretum, Jamaica Plain, Massachusetts 02130.

ANN. MISSOURI BOT. GARD. 63: 399–418. 1976.

Olacaceae, but have been recognized as a distinct family or families by recent monographers and systematists. The Asian genera *Irvingbaileya* and *Cardiopteris* have been suggested to represent distinctive families. The family Icacinaceae has been placed in the Celastrales with a supposed close relationship to the Celastraceae and Aquifoliaceae, a position based on the occasional presence of a basal symmetrical or asymmetrical disc. There is no comparison possible in either of these families to the unusual fruit types found in many genera of the Icacinaceae, and the true relationship of the family remains unclear.

The most primitive member of the family, *Emmotum*, a genus of South America, has 3–5 fertile cells to the fruit. Lianas with anomalous wood structure are most common in Africa and tropical Asian areas.

Developmental stages of the fruit are needed for the proper evaluation of the species described in *Calatola* and *Discophora*. The hard endocarp or putamen of *Calatola* is crested and rugose, and the patterns of sculpturing previously used in identification are often obscured by the dried fleshy outer tissues of the drupe. The range of fruit size for *Discophora*, as well as the nature, taste, and function of the pulvinus, which is a cushion or fleshy appendage developed on the asymmetrical fruit, is not clear. Malpighiaceous, or T-shaped single-celled hairs, are found in *Calatola*, *Leretia*, and *Mappia*, and are characteristic and often overlooked. The genus *Citronella* is unusual in having scorpioid or secund lateral inflorescence branches, and these are strongly curved in flower and fruit. The drupe of *Citronella* has a well-developed radial partition or dissepiment extending often to the center of the locule. The single mature seed is developed around this partition and is hippocrepiform or horseshoe shaped in cross-section. Descriptions are based primarily on extraterritorial material, for no taxon is represented adequately in Panama collections to permit compilation of a complete description.

In the New World some South American species, e.g., *Poraqueiba*, are reported to have edible fruits. Reports concerning *Calatola* suggest the seeds may be edible when roasted, but other reports indicate these can be toxic, causing nausea and vomiting and severe purgative action. Specimens of several genera turn black on drying, and the leaves of these are reported to be used in dyeing cloth.

Literature:

Baas, P. 1974. Stomatal types in Icacinaceae. Additional observations on genera outside Malesia. Acta Bot. Neerl. 23: 193–200.

Bailey, I. W. & R. A. Howard. 1941. The comparative morphology of the Icacinaceae. I. Anatomy of the node and internode. J. Arnold Arbor. 22: 125–132.

——— & ———. 1941. II. Vessels. J. Arnold Arbor. 22: 171–187.

——— & ———. 1941. III. Imperforate tracheary elements and xylem parenchyma. J. Arnold Arbor. 22: 432–442.

——— & ———. 1941. IV. Rays of the secondary xylem. J. Arnold Arbor. 22: 556–568.

Dahl, A. O. 1952. The comparative morphology of the Icacinaceae. VI. The pollen. J. Arnold Arbor. 33: 252–286.

Heintzelman, C. E., Jr. & R. A. Howard. 1948. The comparative morphology of the Icacinaceae. V. The pubescence and the crystals. Amer. J. Bot. 35: 42–52.

Lobreau-Callen, D. 1972. Les Pollen des Icacinaceae: I. Atlas. Pollen & Spores 14: 345–388.

———. 1973. II. Observations en microscopic électronique, corrélations, conclusions. Pollen & Spores 15: 47–89.

Sleumer, H. 1969. Materials towards the knowledge of the Icacinaceae of Asia, Malesia, and adjacent areas. Blumea 17: 181–264.

Staveren, M. G. C. van & P. Baas. 1973. Epidermal leaf characters of the Malesian Icacinaceae. Acta Bot. Neerl. 22: 329–359.

Key to Flowering Material

a. Flowers and plants completely unisexual.
  b. Staminate inflorescences spicate, pistillate inflorescences cymose, few flowered; flowers 4-parted; filaments glabrous; pistillate rudiment absent; pistils pubescent without a basal pulvinus; fruits not flattened but laterally keeled with prominent endocarp reticulations, lacking lateral pulvinus; all parts turning black on drying ---------- 1. *Calatola*
  bb. Both inflorescences cymose; flowers 5-parted; filaments with a pubescent appendage; pistillate rudiment present in staminate flowers; pistils glabrous with a basal fleshy pulvinus; fruits strongly compressed and ridged on the convex surface, the concave surface with fleshy pulvinus; drying dark or not ---------- 4. *Discophora*
aa. Flowers perfect or occasionally polygamous.
  c. Inflorescences extra-axillary often opposing the leaves, the panicle branches short, cymose, the flowers secund; ovary and fruit with a protruding partition, the mature seed hippocrepiform around the partition ---------- 2. *Citronella*
  cc. Inflorescences axillary or terminal, the flowers not secund; ovary and fruit without a protruding partition.
    d. Petals glabrous on the adaxial face; pubescence stellate; foliage darkening on drying ---------- 3. *Dendrobangia*
    dd. Petals pubescent on the adaxial face; pubescence simple or of malpighiaceous hairs; foliage not darkening on drying.
      e. Ovary subtended by a disc; leaves with domatia in the axils of the primary veins ---------- 6. *Mappia*
      ee. Ovary without a disc; leaves lacking domatia.
        f. Trees; locule glabrous inside ---------- 7. *Poraqueiba*
        ff. Vines or shrubs with scrambling branches; locule pubescent inside ---------- 5. *Leretia*

Key to Fruiting Material

a. Fruits compressed laterally, bearing a fleshy pulvinus on the concave face .. 4. *Discophora*
aa. Fruits without fleshy lateral appendage, round in transection.
  b. Locule subdivided, with a radial partition extending toward the center; seed hippocrepiform in section ---------- 2. *Citronella*
  bb. Locule without a protruding partition; seed not hippocrepiform in section.
    c. Locule pubescent inside; lianas ---------- 5. *Leretia*
    cc. Locule glabrous inside; trees.
      d. Embryo minute, less than $\frac{1}{10}$ the length of the seed; foliage turning black on drying.
        e. Putamen strongly reticulate-crested outside; fruit pubescent with simple hairs, becoming glabrate ---------- 1. *Calatola*
        ee. Putamen essentially smooth; fruit stellate-pubescent .... 3. *Dendrobangia*
      dd. Embryo $\frac{1}{2}$–$\frac{3}{4}$ the length of the seed; foliage not drying black.
        f. Mesocarp dry ---------- 6. *Mappia*
        ff. Mesocarp oily ---------- 7. *Poraqueiba*

1. CALATOLA

Calatola Standley, Contr. U.S. Natl. Herb. 23: 688. 1923. TYPE: *Calatola mollis* Standley.

Trees, dioecious. *Leaves* papery to coriaceous, turning black on drying, the margin entire, revolute or sinuate-dentate on juvenile foliage or that of adventitious shoots, the veins oblique-arcuate, slender. Staminate *inflorescences* axillary, densely flowered spikes; pistillate inflorescences few-flowered, axillary racemes or solitary flowers. Staminate *flowers* with the calyx minute, 4-lobed, the corolla gamopetalous, 4-parted, the midrib prominent adaxially, villous, the stamens erect, the filament short, adnate to corolla tube, the anthers oblong, basifixed; pistillate flowers with the calyx 4-lobed, the petals minute, the pistil cylindric, strigose or hirsute, the style not evident. *Fruits* drupaceous, the pericarp thick, fleshy, the putamen bicrestate or winged, irregularly reticulate-dentate or crested or essentially smooth; seed 1, the embryo minute, the endosperm copious.

Calatola is a genus of 7 species of Central America and northern South America. The taxa are poorly defined, mostly on the shape and the ornamentation of the putamen. The developmental stages of the fruit and the variation in ornamentation are not known. Flowering specimens available for study are few and mostly staminate. Additional collections of flowers and fruit from the same pistillate tree are much desired. A mass collection of fruit is essential for an understanding of putamen variation. The characteristics of leaf pubescence used by Sleumer do not appear to be valid.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae IV: Consideration of the New World genera. Contr. Gray Herb. 142: 13–20.

Sleumer, H. 1940. Beiträge zur Kenntnis der Icacinaceen und Peripterygiaceen. Notizbl. Bot. Gart. Berlin-Dahlem 15: 247–250.

1. **Calatola costaricensis** Standley, J. Wash. Acad. Sci. 16: 416. 1926. TYPE: Costa Rica, *Standley & Valerio 50000* (US-1251510, holotype).—FIG. 1.

Trees 6–15 m tall; branches minutely pubescent to glabrate. *Leaves* with petioles 2–5 cm long; blades oblong to elliptic-oblong, 10–25 cm long, 4.5–10.5 cm wide, appressed-pubescent becoming glabrate except in the axils of the veins, the apex short-acuminate to obtuse, the base acute, the primary veins 6–8 pairs. Staminate *spikes* to 13 cm long; rachis and calyx hirsute. Pistillate *flowers* unknown. Drupes ellipsoid to subglobose, 4–6.5 cm long, 3.5–4.0 cm in diam., rounded or obtuse at both ends, stone (putamen) drying bicrestate with several sharp longitudinal crests, with less prominent transverse reticulate ridges; seed 1.

Information is needed on all characteristics of this plant. Fruits are seldom attached to branches, and in many cases appear as though collected from the ground and dried along with casually collected branches. Leaf variation is not

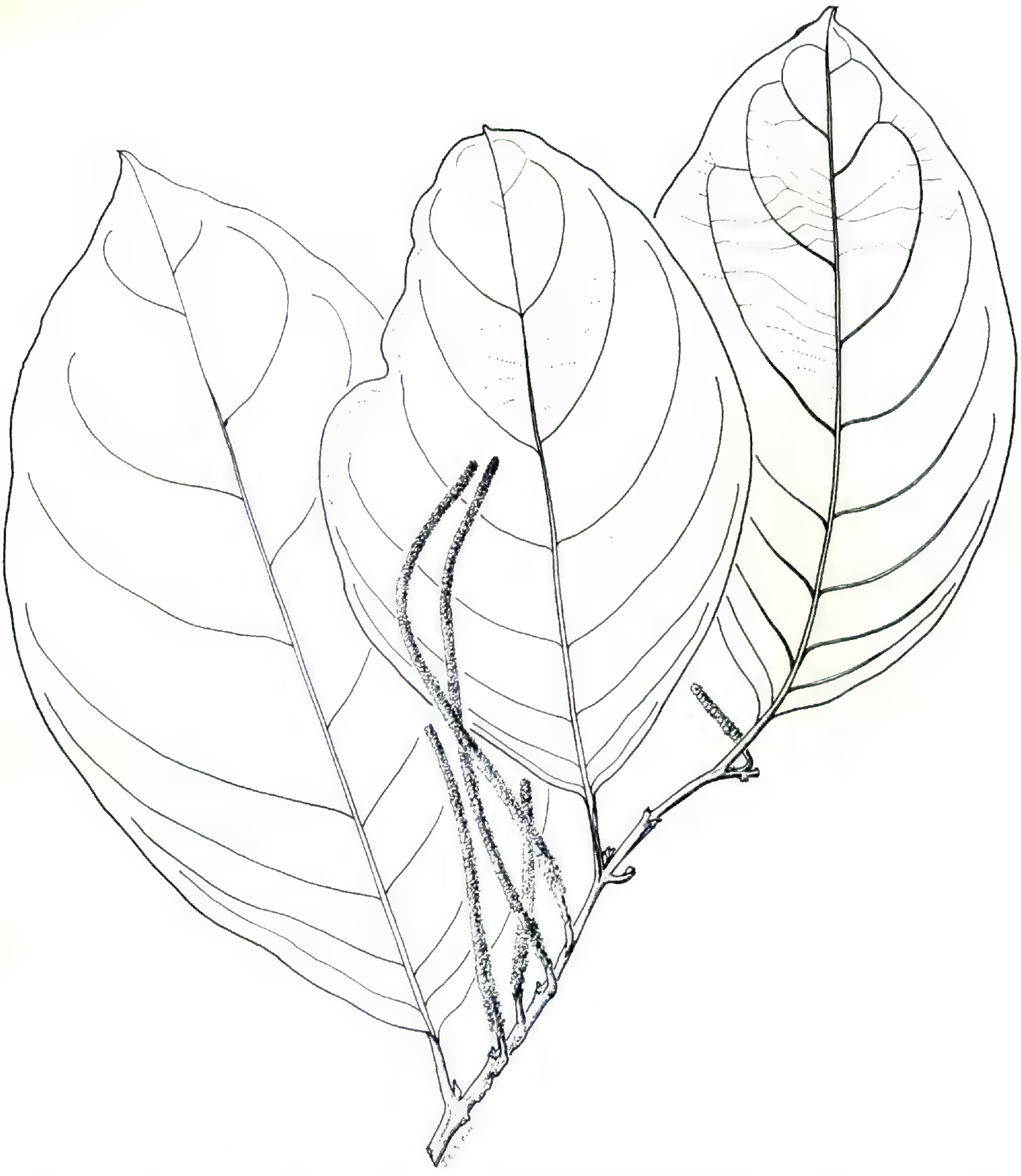

FIGURE 1. *Calatola costaricensis* Standley, habit (×½). [After *Bristan 1227* (MO).]

known. The seeds are reported to be edible if roasted, but to cause nausea and produce violent abdominal pains if eaten raw. It has been collected in flower in December and in fruit in February, March, and August. The common name is "jaquey."

BOCAS DEL TORO: Robalo trail, N slopes of Cerro Horqueta, *Allen 4972* (GH, MO). Almirante, Daytonia farm, *Cooper 371* (F, GH, NY, US). COCLÉ: La Mesa, N of El Valle, *Gentry 6812* (A). DARIÉN: Cerro Pirre, *Bristan 1227* (MO). VERAGUAS: NW of Santa Fe, *Mori & Kallunki 4837* (MO), *6206* (A, MO). NE of Altos de Pacora, *Mori & Kallunki 4947* (MO).

Asterolepidion elatum Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 207. 1922. TYPE: not selected.
Clavapetalum elatum (Ducke) Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 116. 1925.

Trees to 40 m tall; bark smooth, brownish gray; branches stout, ferruginous-tomentose or -stellate pubescent, glabrescent. *Leaves* with petioles 1–1.5 cm long, narrowly canaliculate, stellate-pubescent; blades lance-oblong to obovate, 8–14 cm long, 3–5 cm wide, coriaceous, dark green turning black on drying, glabrate above, persistently ferruginous-stellate pubescent beneath, the apex obtusely acuminate with a curved acumen or acute, the base acute to rounded, the midrib sulcate above, the primary veins 6–8 pairs, irregularly falcate-ascending, slightly anastomosing near the margin. *Inflorescences* paniculate, 3–4 cm long, much branched, the branches stellate-pubescent, the bracts lance-ovate, fleshy, densely pubescent and ciliate. *Flowers* perfect; sepals 1–2 mm long, stellate-pubescent and ciliate; corolla white, 3 mm long, the lobes inflexed in bud with clavate or oblanceolate apical appendages, reflexed at maturity; ovary 0.4 mm high and 0.6 mm diam., bearing large stellate hairs, the style minute, the stigma capitate, minute. *Drupes* compressed, 1.5–2 cm long, 1 cm wide, 0.5 cm thick, sparsely stellate-pubescent, the putamen thin and essentially smooth on both surfaces; seed 1.

This is the first record for the taxon from Panama. Material seen was collected in flowering condition in March, and the description is compiled from extra-territorial material.

PANAMÁ: Road from El Llano to Cartí-Tupile, 12 mi above the Pan-Am. Hwy., 200–500 m, *Liesner 680* (MO).

4. DISCOPHORA

Discophora Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 118. 1852. TYPE: *D. guianensis* Miers.

Kummeria Mart. ex Engl., Fl. Bras. 12(2): 52. 1872. TYPE: *K. brasiliensis* Mart.

Trees or *shrubs*; branches short strigose-pubescent or glabrate; bark smooth. *Leaves* alternate, entire. *Inflorescences* axillary, paniculate with strong branches at the base, the panicle diffuse, elongate and divaricate in fruit; pedicels strigose-pubescent, bracteate. *Flowers* polygamous or possibly unisexual; calyx short-campanulate, broadly and unevenly 5-lobed, the lobes deltoid or reduced to teeth; petals free, essentially glabrous, the apices inflexed with short mucros, the midrib prominent adaxially; stamens with fleshy flattened filaments bearing an adaxial swelling or appendage midway along its length, the appendage with clavate hairs, the filament abruptly narrowed below the versatile anthers, the anther sacs ovate, diverging at the base; pistil in staminate flowers abortive, cylindrical or slightly conical, either immersed in a fleshy disc or eccentrically placed in the orifice of a hippocrepiform (U-shaped) disc, the ovary in functional pistillate flowers cylindrical or angled and slightly compressed bearing a lateral basal fleshy avascular pulviniform appendage, the style not evident, the stigma capitate, occasionally broader than the ovary, the ovules 2, nearly collateral, pendant from the apex of the locule. *Fruits* drupaceous, flattened, slightly arcuate, bear-

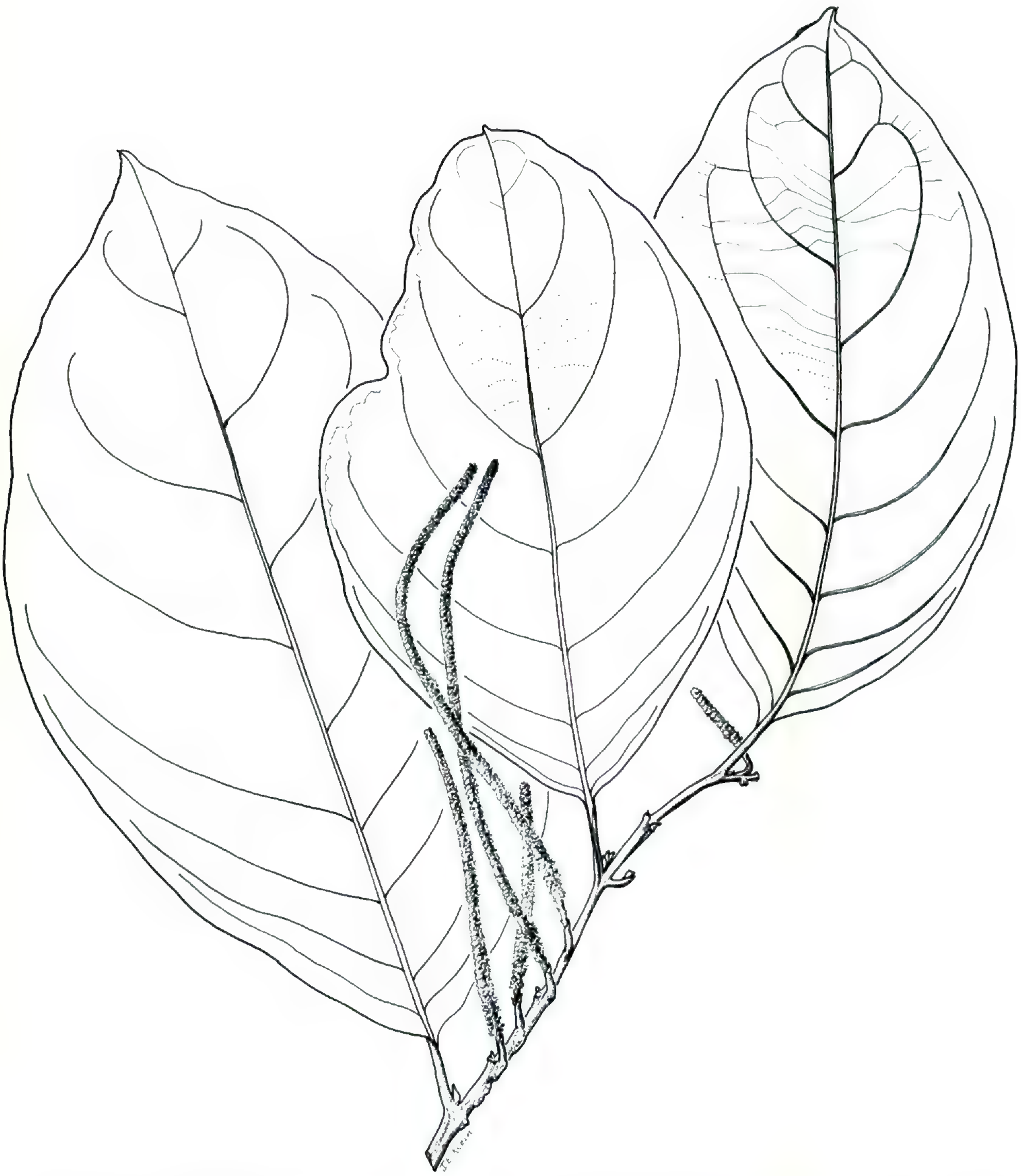

FIGURE 1. *Calatola costaricensis* Standley, habit ($\times \frac{1}{2}$). [After *Bristan 1227* (MO).]

known. The seeds are reported to be edible if roasted, but to cause nausea and produce violent abdominal pains if eaten raw. It has been collected in flower in December and in fruit in February, March, and August. The common name is "jaquey."

BOCAS DEL TORO: Robalo trail, N slopes of Cerro Horqueta, *Allen 4972* (GH, MO). Almirante, Daytonia farm, *Cooper 371* (F, GH, NY, US). COCLÉ: La Mesa, N of El Valle, *Gentry 6812* (A). DARIÉN: Cerro Pirre, *Bristan 1227* (MO). VERAGUAS: NW of Santa Fe, *Mori & Kallunki 4837* (MO), *6206* (A, MO). NE of Altos de Pacora, *Mori & Kallunki 4947* (MO).

2. CITRONELLA

Citronella D. Don, Edinburgh New Philos. J. 13: 243. 1832. TYPE: *Villaresia mucronata* Ruiz & Pavón.

Villaresia Ruiz & Pavón, Fl. Peruv. Chil. 3: 9, *tab. 231.* 1803, non Fl. Peruv. Chil. Prodr. 35. 1793.

Briquetina Macbride, Field Mus. Nat. Hist., Bot. Ser. 11: 26. 1931. TYPE: *Briquetina incarum* Macbride.

Trees or *shrubs*; branches occasionally scandent. *Leaves* coriaceous or submembranous, entire, the veins oblique-arcuate and anastomosing. *Inflorescences* terminal, axillary, extra-axillary or supra-axillary, paniculate, the branches commonly secund or scorpioid. *Flowers* perfect or polygamous; calyx fleshy, persistent; petals free, fleshy, the apices inflexed, the midrib prominently developed; stamens free, the filaments fleshy, glabrous, more or less flattened, the anthers basifixed, introrse, longitudinally dehiscent; disc wanting; ovary subgibbose, commonly 1-loculed, the locule with a prominent parietal ridge, the ovules 2, pendant from near the apex, the style glabrous, rudiments frequently present, the stigma capitate. *Drupes* scarcely fleshy, the putamen woody, the locule incompletely septate; seed solitary, longitudinally folded around the vertical woody dissepiment, hippocrepiform in section, the embryo small, the endosperm copious.

Citronella is a genus of 20 species in 2 sections: one of the Western Hemisphere, from Costa Rica and Panama throughout South America, but not the West Indies; and the other from the Old World, from the Philippines, East Indies, New Caledonia, Polynesia, New Guinea, and Australia, but not continental Asia. The secund-scorpioid inflorescence branches and the structure of the fruit with a hippocrepiform seed are unique in the family.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae V: A revision of the genus *Citronella* D. Don. Contr. Gray Herb. 142: 60–92.

Sleumer, H. 1940. Beiträge zur Kenntnis der Icacinaceen und Peripterygiaceen. Notizbl. Bot. Gart. Berlin-Dahlem 15: 228–257.

1. **Citronella costaricensis** (Donnell Smith) Howard, J. Arnold Arbor. 21: 471. 1940.—FIG. 2.

Villaresia costaricensis Donnell Smith, Bot. Gaz. (Crawfordsville) 31: 110. 1901. TYPE: Costa Rica, *Tonduz 11664* (US-1394149, holotype).

Trees to 20 m tall; branches sparsely strigose to glabrate. *Leaves* with petioles 8–15 mm long; blades lanceolate-elliptic to oblong-elliptic, 9–16 cm long, 4–6 cm wide, coriaceous, shining above, gray and dull beneath when dry, sparsely strigose, becoming glabrate, the apex acuminate or acute, the base acute or rounded, the margin entire. *Inflorescences* extra-axillary, commonly opposing the leaf, paniculate, 9–17 cm long with branches secund-scorpioid to 1 cm long. *Flowers* sessile, polygamous; calyx 2 mm diam., the lobes triangular and obtuse,

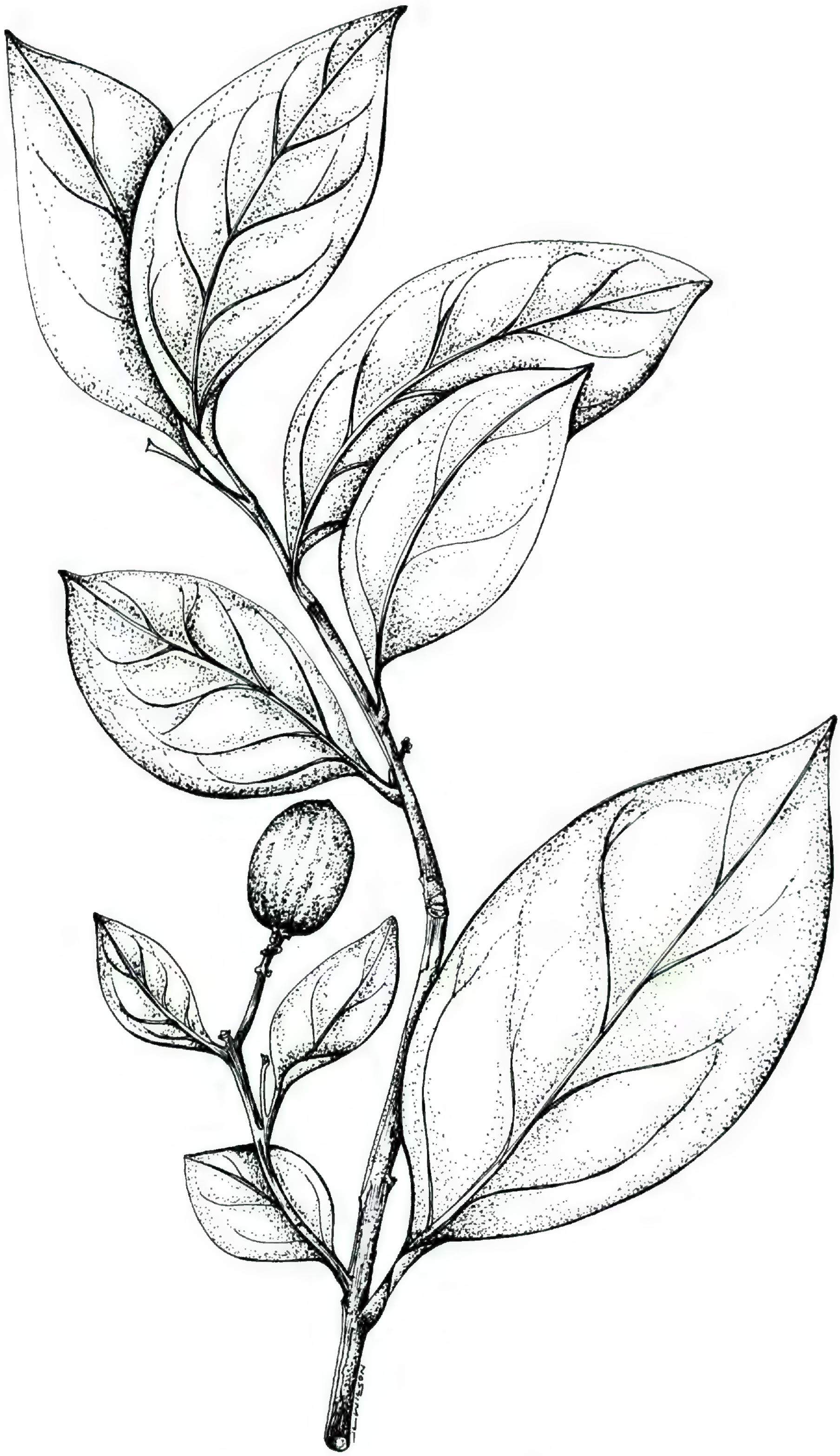

FIGURE 2. *Citronella costaricensis* (Donnell Smith) Howard, habit ($\times 7/10$). [After *Hatheway 1283* (MO), Costa Rica.]

0.6-0.8 mm long, 1 mm wide; petals oblong-elliptic, 3.5 mm long, 1.5–2 mm wide, glabrous; fertile stamens 2.6–3 mm long, the sterile stamens shorter than the ovary; fertile pistil 2.5 mm long, the ovary globose, hirsute, the style glabrous, the sterile pistil 1–1.2 mm long, hirsute. *Drupes* elliptic-obloid, 2–3.5 cm long, 1.3–1.8 cm diam., the apex asymmetrically apiculate, the putamen longitudinally ridged.

This species occurs in Panama and Costa Rica. The plant was collected in Chiriquí at 1,500–1,600 m, comparable to its locations in Costa Rica. The leaves of the plants from Costa Rica have few to many axillary pores or domatia. Only 2 domatia were observed on the leaves of the specimen from Panama, although tissue in the axils of some primary veins showed a variation in the pattern of the epidermal cells, suggesting that if the proper insect were present, a domatium might be formed.

CHIRIQUÍ: Santa Clara region, 27 km NW of El Hato del Volcán, *Mori & Bolten 7217* (A, MO).

3. DENDROBANGIA

Dendrobangia Rusby, Mem. Torrey Bot. Club 6: 19. 1896. TYPE: *D. boliviana* Rusby.

Clavapetalum Pulle, Recueil Trav. Bot. Néerl. 9: 148. 1912. TYPE: *C. surinamense* Pulle.
Asterolepidion Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 207. 1922. TYPE: *A. elatum* Ducke.

Trees; branches terete, lepidote-strigose to glabrate. *Leaves* alternate, entire. *Inflorescences* axillary, paniculate, diffuse, densely pubescent. *Flowers* sessile in glomerules of 3–5, perfect; calyx 5-parted, fleshy, the segments stellate-pubescent, coherent at the base, imbricate; corolla united at the base, 5-lobed, valvate, glabrous or rarely papillate, the inflexed apices with long clavate appendages; stamens 5, the filaments glabrous, dilated at the base, adnate to the corolla tube at the sinuses, the anther sacs elongate, diverging at the base; disc none; ovary dorso-ventrally compressed, stellate-pubescent, uniloculate, the ovules 2, collateral, the style stout, the stigma capitate, minute. *Fruits* drupaceous, the mesocarp thin and fleshy, the putamen thin and woody; seed solitary, the embryo minute, the endosperm copious.

Although the original description contains no dedication, Rusby's publication concerns the plants collected in Bolivia by Miquel Bang, and the genus apparently honors the collector.

The taxon has not been recollected in Bolivia, but subsequent collections have been made in French Guiana, Guyana, Surinam, Venezuela, Ecuador, and Brazil (Amazonas). This is the first record from Panama.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae IV: Consideration of the New World Genera. Contr. Gray Herb. 142: 38–41.

FIGURE 3. *Dendrobangia boliviana* Rusby, habit (×½). [After *Liesner 680* (MO).]

1. **Dendrobangia boliviana** Rusby, Mem. Torrey Bot. Club 6: 19. 1896. TYPE: Bolivia, *Rusby 1684* (NY).—FIG. 3.

Clavapetalum surinamense Pulle, Recueil Trav. Bot. Néerl. 9: 148. 1912. TYPE: Surinam, *Pulle 89* (not seen).

Asterolepidion elatum Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 207. 1922. TYPE: not selected.
Clavapetalum elatum (Ducke) Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 116. 1925.

Trees to 40 m tall; bark smooth, brownish gray; branches stout, ferruginous-tomentose or -stellate pubescent, glabrescent. *Leaves* with petioles 1–1.5 cm long, narrowly canaliculate, stellate-pubescent; blades lance-oblong to obovate, 8–14 cm long, 3–5 cm wide, coriaceous, dark green turning black on drying, glabrate above, persistently ferruginous-stellate pubescent beneath, the apex obtusely acuminate with a curved acumen or acute, the base acute to rounded, the midrib sulcate above, the primary veins 6–8 pairs, irregularly falcate-ascending, slightly anastomosing near the margin. *Inflorescences* paniculate, 3–4 cm long, much branched, the branches stellate-pubescent, the bracts lance-ovate, fleshy, densely pubescent and ciliate. *Flowers* perfect; sepals 1–2 mm long, stellate-pubescent and ciliate; corolla white, 3 mm long, the lobes inflexed in bud with clavate or oblanceolate apical appendages, reflexed at maturity; ovary 0.4 mm high and 0.6 mm diam., bearing large stellate hairs, the style minute, the stigma capitate, minute. *Drupes* compressed, 1.5–2 cm long, 1 cm wide, 0.5 cm thick, sparsely stellate-pubescent, the putamen thin and essentially smooth on both surfaces; seed 1.

This is the first record for the taxon from Panama. Material seen was collected in flowering condition in March, and the description is compiled from extra-territorial material.

PANAMÁ: Road from El Llano to Cartí-Tupile, 12 mi above the Pan-Am. Hwy., 200–500 m, *Liesner 680* (MO).

4. DISCOPHORA

Discophora Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 118. 1852. TYPE: *D. guianensis* Miers.

Kummeria Mart. ex Engl., Fl. Bras. 12(2): 52. 1872. TYPE: *K. brasiliensis* Mart.

Trees or *shrubs*; branches short strigose-pubescent or glabrate; bark smooth. *Leaves* alternate, entire. *Inflorescences* axillary, paniculate with strong branches at the base, the panicle diffuse, elongate and divaricate in fruit; pedicels strigose-pubescent, bracteate. *Flowers* polygamous or possibly unisexual; calyx short-campanulate, broadly and unevenly 5-lobed, the lobes deltoid or reduced to teeth; petals free, essentially glabrous, the apices inflexed with short mucros, the midrib prominent adaxially; stamens with fleshy flattened filaments bearing an adaxial swelling or appendage midway along its length, the appendage with clavate hairs, the filament abruptly narrowed below the versatile anthers, the anther sacs ovate, diverging at the base; pistil in staminate flowers abortive, cylindrical or slightly conical, either immersed in a fleshy disc or eccentrically placed in the orifice of a hippocrepiform (U-shaped) disc, the ovary in functional pistillate flowers cylindrical or angled and slightly compressed bearing a lateral basal fleshy avascular pulviniform appendage, the style not evident, the stigma capitate, occasionally broader than the ovary, the ovules 2, nearly collateral, pendant from the apex of the locule. *Fruits* drupaceous, flattened, slightly arcuate, bear-

FIGURE 4. *Discophora guianensis* Miers, habit (×½). [After *Correa 809* (MO).]

ing a large oblong fleshy appendage of a lighter color on the concave side, the pericarp dark-pigmented, fleshy, the putamen with 2 pairs of equal primary ribs on the lateral edges of the fruit and 1 median ridge developed on both the concave and convex sides, the intermediate ridges more or less completely and prominently developed on the convex side; seed 1, embryo minute.

Discophora is a genus of 2 species occurring in Brazil, British Guiana, Colombia, and Peru. The cream-colored lateral pulvinus on the otherwise green, asymmetrical fruit is unusual in the family, occurring only in this genus in the New World. No data are available on the taste of the pulvinal tissue or on its possible role in the distribution of the fruit.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae IV: Consideration of the New World Genera. Contr. Gray Herb. 142: 21–30.

1. **Discophora guianensis** Miers, Ann. Mag. Nat. Hist., ser. 2, 10: 118. 1852. TYPE: British Guiana, *Parker s.n.* (K).—FIG. 4.

Kummeria brasiliensis Mart., Herb. 1276. 1837, nomen; Mart. ex Engl., Fl. Bras. 12(2): 52. 1872. TYPE: Brazil, *Martius 1276* (M).

Lasianthera amazonica Barbosa Rodriques, Vellosia 1: 12. 1891. TYPE: Brazil, *Rodriques 337* (not seen).

Discophora panamensis Standley, Publ. Field Columbiam Mus., Bot. Ser. 4: 222. 1929. TYPE: Panama, *Cooper 613* (US-1486713, holotype).

Trees or *shrubs* to 13 m tall; trunk to 10 cm diam.; branches lightly golden strigose. *Leaves* with petioles 10–25 cm long, stout, canaliculate, strigose to glabrate; blades oblong-lanceolate to elliptic-oblong, 15–30 cm long, 7–13 cm wide, coriaceous, olive brown, silvery- or golden-sericeous or pilose when young, becoming glabrate, the apex acute or acuminate with an acumen to 4 cm long and ultimately rounded, the base acute, rarely rounded, the primary veins 7–10 pairs, arcuate or ascending, the ultimate veins conspicuously reticulated and sharply prominent on both surfaces. *Inflorescences* paniculate, strongly branched from the base, rarely strict, densely golden-strigose, becoming glabrate and stout in fruit, the bracts lance-ovate or ovate, densely pubescent. *Flowers* with calyx campanulate, glabrous except for the apices of the teeth; petals cream yellow, obovate to elliptic, 2–3 mm long, glabrous except for minute pubescence on the inside of the inflexed acumen; functional stamens 3.5–4 mm long, the anthers broadly ovate, to 0.7 mm long, the stamens of pistillate flowers much smaller; functional pistil cylindrical or slightly angular and arcuate, 3 mm high, the basal lateral fleshy pulvinus to 1 mm high and surrounding about half of the ovary. *Fruits* drupaceous, 1–2 cm long, 0.8–1.0 cm wide, 0.9 cm thick, the putamen strongly 5-ribbed on the convex side.

Discophora panamensis originally was considered distinct on the basis of smaller leaves and more slender staminate inflorescences. Additional collections suggest these characteristics are not of taxonomic value. *Discophora guianensis* has been collected in Panama in flower in February, March, April, and May, and in fruit in July and August.

BOCAS DEL TORO: Almirante, Buena Vista Camp on Chiriquí Trail, *Cooper 613* (FM, GH, US). Chiriquí Lagoon, Fish Creek Mountains, *von Wedel 2225* (GH, MO). CANAL ZONE: Near Maru Towers, *Johnston 1504* (A, MO). Pavón Road, *Johnston 1539* (A, MO). DARIÉN: Pirre, *Bristan 1230* (MO, OS); *Duke & Elias 13671* (MO). PANAMÁ: 11 km above Pan-Am. Hwy. from El Llano to Cartí-Tupile, *Kennedy & Dressler 2950* (A, MO); *Kennedy et al. 3111* (A); *Liesner 1176* (A, MO). SAN BLAS: El Llano-Cartí road, 24.5–25 km from Interam. Hwy., *Mori & Kallunki 5532* (A, MO).

5. LERETIA

Leretia Vell., Fl. Flum. 99. 1825; Fl. Flum. Ic. 3: *tab.* 2. 1827. TYPE: *L. cordata* Vell.

Lianas, *shrubs* or small *trees* with scrambling branches. *Leaves* alternate, short-petioled, entire. *Inflorescences* axillary, much-branched cymes or panicles. *Flowers* articulated to short-bracteate pedicels, perfect, rarely unisexual by abortion; calyx lobes 5, subacute to rounded; petals 5, free, valvate with inflexed tips; stamens 5, the filaments filiform, the connective extended to an inconspicuous tip; pistil asymmetrical, usually with 2 rudimentary styles, the functional style glabrous, the stigma capitate, the ovary hirsute with a columnar base, the ovules 2. *Fruits* drupaceous, glabrate, ovoid ellipsoid, slightly flattened, the apex obliquely umbonate, the mesocarp thin, the putamen tenuous, smooth; seed 1, the embryo with wrinkled cotyledons, the endosperm present.

A single polymorphic species has been collected in Brazil, British Guiana, Venezuela, and Peru.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae II. *Humirianthera*, *Leretia*, *Mappia* and *Nothapodytes*, valid genera of the Icacineae. J. Arnold Arbor. 23: 55–78.

1. **Leretia cordata** Vell., Fl. Flum. 99. 1825. TYPE: Brazil, *Vellozo* (not seen). —FIG. 5.

L. vellozii Miers, Ann. Mag. Nat. Hist., ser. 2, 9: 392. 1852, nom. illeg.
L. nitida Miers, Ann. Mag. Nat. Hist., ser. 3, 4: 365. 1859. TYPE: Brazil, *Spruce 1528* (K).
Mappia poeppigiana Baillon, Adansonia 11: 175. 1874. TYPE: Peru, *Poeppig 2339* (P).
Leretia poeppigiana (Baillon) Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 15: 245. 1940.
L. glabrata Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 15: 245. 1940. TYPE: Brazil, *Ducke 29028* (B, not seen).

Lianas or small *trees* with scrambling branches; branches short-strigose pubescent, becoming glabrate, the old branches with dark brown corky bark. *Leaves* with petioles stout, commonly twisted, 0.8–1.5 cm long, densely chestnut brown strigose pubescent, corky at maturity; blades ovate-lanceolate to oblong or elliptic, 10–19 cm rarely to 30 cm long, 4–12 cm broad, the apex acute with the apiculate point rounded or obtuse, the base acute or rounded, the upper surface sparsely white pilose-pubescent, soon becoming glabrate, the lower surface with white or yellowish malpighiaceous hairs with almost equal arms, the primary veins 6–8 pairs, arcuate, anastomosing near the margin to form a complex reticulum. *Inflorescences* cymose, to 18 cm long and 10 cm diam., the bracts ovate, acute, strigose-pubescent. *Flowers* with the calyx patelliform, 2 mm diam., the lobes or teeth 0.5–0.8 mm high, densely golden strigose; petals white to cream colored, lanceolate-ovate or oblong, 4.8–5.5 mm long, 1.8–2 mm broad, densely hirsute outside, inside the midrib moderately well developed, long pilose or tomentose, the inflexed apices glabrous; stamens 3–4.5 mm long, glabrous; ovary 1.5 mm diam. at anthesis, the locule densely hirsute or tomentose inside, the functional style 1.5–2.5 mm long, the rudimentary styles rarely 0.3 mm long. *Fruits* (not known from Panama), 3.4–4.5 cm long, 2–2.5 cm wide, 1.5–2 cm thick, the base acute or tapering, the apex acute, densely hirsute when young, becoming glabrate, the putamen papery, sparsely pubescent inside with long pilose hairs; seed 1.

More material, especially of the fruit, is needed from Panama. Field observations are needed to determine the growing characteristics of this plant variously described as a liana or a tree with scrambling branches. The variation in size and shape of the leaves is that commonly found in scrambling shoots.

BOCAS DEL TORO: Vic. Chiriquí Lagoon, Fish Creek Hills, *von Wedel 2443* (GH, MO, NY, US). COLÓN: Guásimo, *Croat 9920* (MO). DARIÉN: Río Uruceca, *Bristan 1433* (MO). Río Pirre, 10 mi S of El Real near Dos Bocas, *Foster & Lowenbach 2270* (Duke). Río Pirre, near Pirre, *Gentry & Clewell 6939* (A, MO). Quebrada Camachimuricate near Bartolo, *Kennedy 2853* (MO).

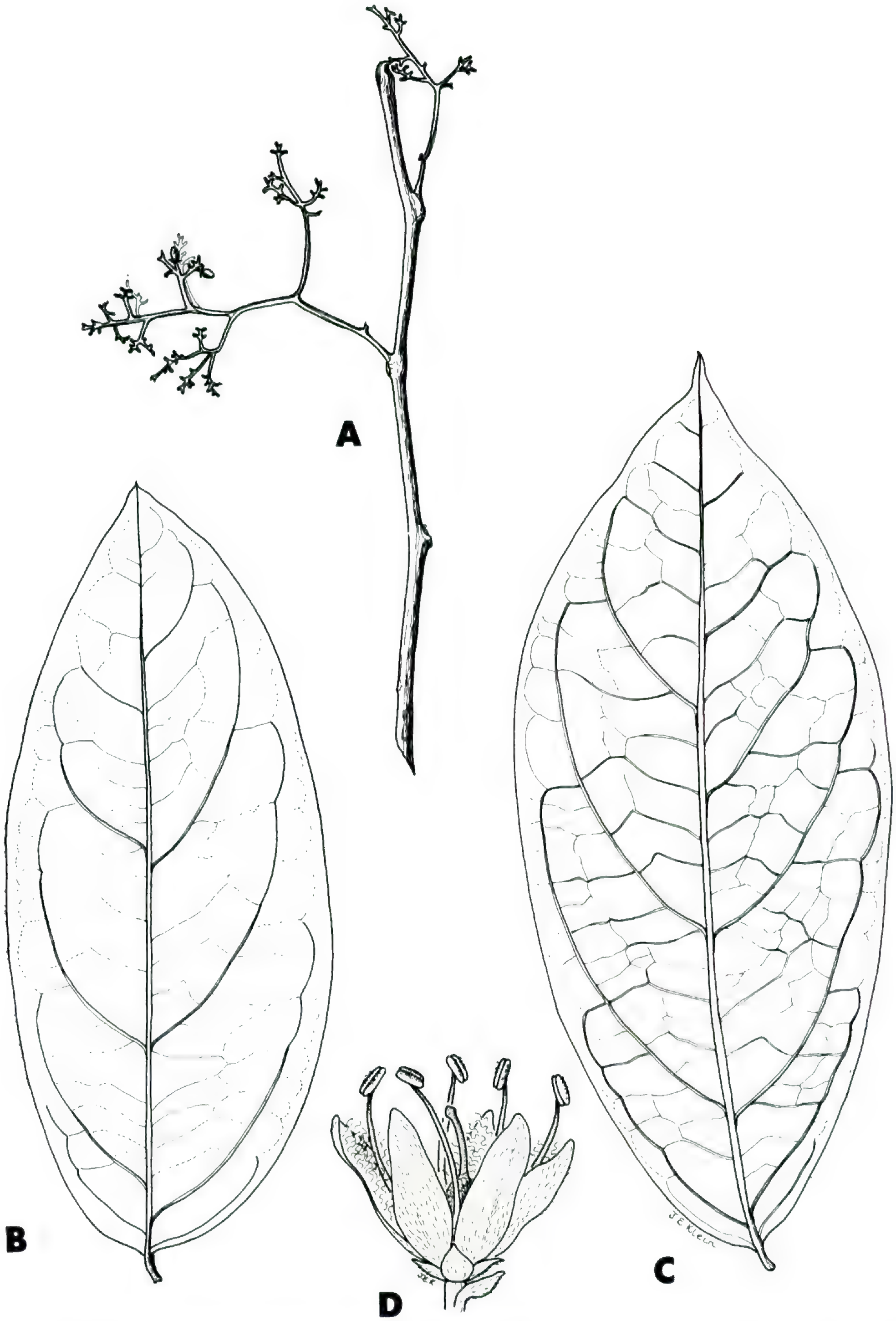

FIGURE 5. *Leretia cordata* Vell.—A. *Inflorescence* (×3/5).—B–C. Leaves (×3/5).—B. Upper side.—C. Lower side. [After *von Wedel 2443* (MO).]—D. Flower (×5 3/5). [After *Kennedy* 2853 (MO).]

6. MAPPIA

Mappia Jacq., Hort. Schoenb. 1: 22, *tab. 47*. 1797, nom. cons. TYPE: *M. racemosa* Jacq.

Trees and *shrubs*. *Leaves* alternate, petiolate, entire with slightly revolute margins, commonly with domatia in the axils of veins on the abaxial surface. *Inflorescences* axillary, cymose or corymbose. *Flowers* perfect, 5-parted; calyx patelliform, minutely toothed; petals valvate, strigose or glabrate outside, villose inside, the apex inflexed, short, glabrous; stamens free, the filaments filiform, flattened, glabrous; basal disc fleshy, hirsute to glabrous on the margin and inside, glabrous outside; pistil symmetrical, the ovary hirsute to glabrous, 1-celled, the ovules 2, pendant from the apex of the locule. *Fruits* drupaceous, the putamen thin, smooth; seed 1, the embryo large, the endosperm abundant.

Mappia is a genus of 5 species in the Greater Antilles, Mexico, Belize, and Guatemala.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae II. *Humirianthera*, *Leretia*, *Mappia* and *Nothapodytes*, valid genera of the Icacineae. J. Arnold Arbor. 23: 55–78.

1. **Mappia racemosa** Jacq., Hort. Schoenb. 1: 22, *tab. 47*. 1797. TYPE: Jacquin, Hort. Schoenb. *tab. 47*.—FIG. 6.

Icacina dubia Macf., Fl. Jam. 1: 122. 1837. TYPE: *Macfadyen* (not seen).
Mappia affinis Miers, Ann. Mag. Nat. Hist., ser. 2, 9: 394. 1852. TYPE: Jamaica, *Purdie* (K).
Leretia racemosa (Jacq.) House, Amer. Midl. Naturalist 8: 62. 1922.

Large *shrubs* or small *trees* to 11 m tall; branches glabrous. *Leaves* with petioles 12–25 mm long, slightly strigose in the sulca, becoming glabrate; blades lanceolate, oblanceolate or oblong, 10–19 cm long, 3–5 cm broad, the apex acuminate or rounded, the base acute to cuneate, glabrous, thin coriaceous, the veins 7–9 pairs, diverging obliquely, scarcely arcuate except near the margin, the axillary domatia sometimes with pubescence. *Inflorescences* with peduncles 1–1.5 times the petiole, densely pilose to glabrate, few to many flowered. *Flowers* with calyx 1.5–2 mm diam., 5-toothed, sparsely strigose with hairs clustered at the teeth; petals cream colored, lanceolate to oblong, 3.4–5 mm long, 0.9–1.1 mm wide, densely strigose to glabrate outside, abundantly pilose to hirsute inside, the pubescence aggregated in the lower third, the apex inflexed, glabrous; stamens 2.5–4.5 mm long; disc fleshy, hirsute on the edge and within, lobed, 0.2–0.3 mm high; pistil 2–3 mm long at anthesis, densely hirsute to glabrate, the style short, glabrous, the stigma capitate, occasionally bilobed. *Fruits* ellipsoidal, 1.4–1.6 cm long, 0.9–1.1 cm wide, tapering to the base or rounded, the apex umbonate, the mesocarp fleshy or fibrous, the putamen smooth to slightly rugose; seed 1, the endosperm apparently oily.

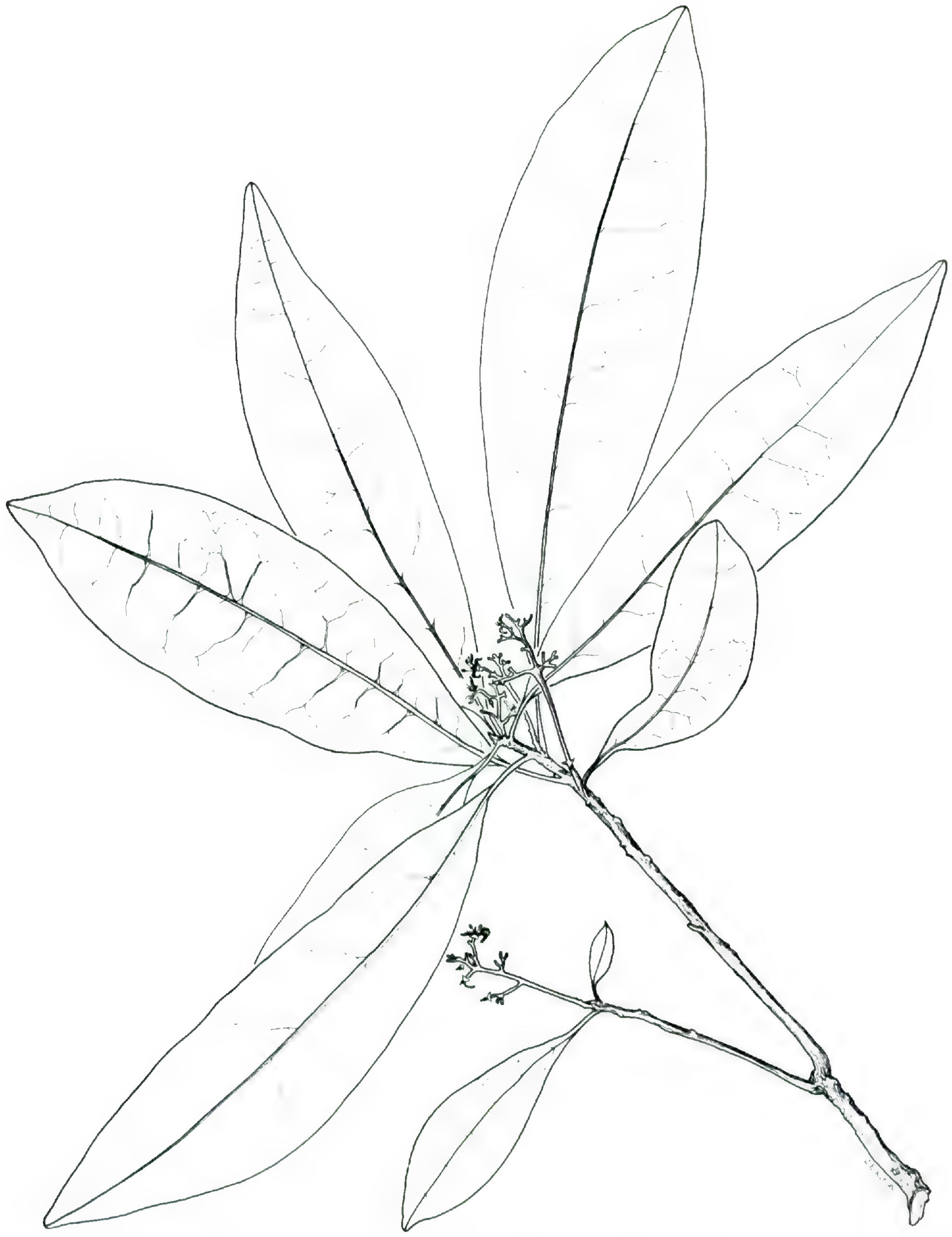

FIGURE 6. *Mappia racemosa* Jacq., habit (×½). [After *Proctor 17475* (MO), Jamaica.]

Jacquin reported that the type collection was made in Jamaica, but the type illustration was apparently drawn from material cultivated in the Schoenbrunn gardens in Vienna. No specimen has been located, and at present the illustration must be considered the holotype.

The species has been collected in Cuba, Jamaica, and Puerto Rico, with a

single collection from Panama. Lundell (Wrightia 4: 139. 1970) described *Mappia multiflora* based on *Gentle 6365* (LL) from Belize and *Contreras 6781* from Guatemala. Neither specimen has been available on loan. The distinguishing characteristics of "larger much-branched inflorescences, smaller flowers, strigillose branchlets and thin membranaceous leaves with more prominent venation" require further study to determine if these Central American representatives are truly distinct from the Antillean plants.

BOCAS DEL TORO: Flat Rock, *Cooper 563* (F, NY, US).

7. PORAQUEIBA

Poraqueiba Aubl., Fl. Guiane 1: 123, *tab. 47*. 1775. TYPE: *P. guianensis* Aubl.

Trees. *Leaves* alternate, coriaceous, entire. *Inflorescences* axillary, paniculate, strongly branched from the base, the flowers subtended by 3 imbricate bracts. *Flowers* perfect; calyx lobes 5, fleshy, lightly imbricated; petals valvate, fleshy, the edges incurved, furrowed inside, more or less white silky-pubescent on the lateral and median ridges, the apices inflexed; stamens with fleshy, flattened filaments concave at the base, glabrous, the anthers basifixed, erect, the connective broadened and extended in an attenuate inflexed apicule; disc none; ovary globose, glabrous, the ovules 2, the style terminal, short, the stigma minute, capitate. *Fruits* drupaceous, ovoid to oblong, more or less oblique, the mesocarp fleshy and oily, the putamen woody and smooth with prominent longitudinal ridges; seed 1.

This genus of 3 species has been collected in Surinam, Brazil, Peru, and Panama.

Literature:

Howard, R. A. 1942. Studies of the Icacinaceae IV. Consideration of the New World genera. Contr. Gray Herb. 142: 49–58.

1. **Poraqueiba guianensis** Aubl., Fl. Guiane 1: 123, *tab. 47*. 1775. TYPE: *Aublet* (P, not seen).—FIG. 7.

Poraqueiba surinamensis Miers, Ann. Mag. Nat. Hist., ser. 2, 9: 483. 1852. TYPE: Surinam, *Hostman 1209* (K).

Trees to 25 m; bark ash gray. *Leaves* with petioles 1.2–1.5 cm long, canaliculate, commonly twisted; blades oblong, 15–25 cm long, 6–8 cm wide, thinly coriaceous, lightly sericeous below, becoming glabrate, the apex long attenuate or acuminate, the base acute or rarely obtuse, veins 7–8 pairs, prominent. *Inflorescences* paniculate; calyx with obtuse, ovate lobes 1 mm long and broad, pilose; petals ovate to lance-ovate, 3.1–3.4 mm long, 1.1–1.2 mm broad, fleshy, pilose outside, bearing 2 grooves in the upper half and 3 below which are separated by a strigose or pilose transverse ridge; stamens 2.7–2.8 mm long, the anther sacs noticeably marginal and not confluent; ovary globose, glabrous, 1.2–1.5 mm diam., the style short, 0.2–0.5 mm long. *Fruits* drupaceous, 2.5 cm long, 1.3–1.6 cm in diam., the mesocarp with oil-bearing cells; seed 1.

FIGURE 7. *Poraqueiba guianensis* Aubl., habit (×½). [After *Elburg 1962* (MO), Surinam.]

This species has been reported from Brazil, Surinam, and Venezuela, with a single collection from Panama. The *Hagen* specimen has a single unattached fruit and no complete leaves. The description is compiled from extraterritorial material.

Lanjouw and Uittien (Recueil Trav. Bot. Néerl. 37: 155. 1940) report that

an Aublet specimen in the Denaiffe Herbarium (P), Vol. 5, no. 176, consists of a single branch with two leaves and no flowers.

A local name is "mamecillo olocoso."

CHIRIQUÍ: Boquete region, Cerro Horqueto, 6,500 ft, *Hagen 2116* (GH, MO, NY).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 108. SAPINDACEAE[2]

THOMAS B. CROAT[3]

Trees, shrubs, lianas or herbaceous *vines. Leaves* alternate, simple, paripinnate, imparipinnate or compound-pinnate; climbing genera with watchspring tendrils, milky sap and usually stipitate leaves and often with composite wood (consisting of two or more separate bundles, usually one central bundle and three peripheral bundles); leaflets entire, dentate or lobate, mostly pinnately veined. *Inflorescences* of thyrses or cincinni disposed in bracteolate racemes or panicles. *Flowers* polygamous or dioecious, regular or irregular, generally small and white; sepals (0) 4 or 5, free or somewhat connate, often unequal, mostly imbricate in bud; petals (0) 3–6, usually clawed, often barbate or squamate within, equal or unequal, imbricate; disc various, commonly annular, complete or incomplete, often glandular; stamens (5–)8(–10), commonly hypogynous and inserted within the disc, the filaments usually filiform or subulate, often villous, the anthers 2-celled, versatile and basifixed, introrse, longitudinally dehiscent; ovary superior, 2(or 3)-locular, (2 or)3-carpellate and lobed accordingly, the styles simple or divided, terminal on the ovary or eccentric, the ovules anatropous, camplytropous or amphitropous, 1 or 2 per locule, affixed to the axis, ascending. *Fruits* capsular or drupaceous, variously dehiscent or indehiscent, entire or lobate, often consisting of 2 or 3 samaras, the carpels often separating at maturity from a central axis; seeds globose or compressed, arillate or naked; endosperm absent; embryo usually thick, often plicate or spirally convolute, the cotyledons usually plano-convex, unequal, the radicle short, inflexed, inferior.

The family Sapindaceae has 150 genera of diverse form and habit. It inhabits all tropical and subtropical regions of the world. The family is divided into two subfamilies, the Sapindoideae (Eusapindaceae) with a single ovule per locule and the Dodonaeoideae (Dyssapindaceae) with 2–several ovules per locule. All but 5 of the 14 tribes and all but about 30 of the 150 genera are in the subfamily Sapindoideae. Most genera are of the Old World, especially Africa and Asia but also Madagascar and Australia.

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[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] Based in part on a preliminary manuscript prepared before 1963 by Calway Dodson, Marie Selby Botanical Garden, 800 South Palm Avenue, Sarasota, Florida 33577. This contribution by Dr. Dodson is gratefully acknowledged.

[3] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

ANN. MISSOURI BOT. GARD. 63: 419–540. 1976.

Thirty-six genera are known from the New World. Of these, *Paullinia*, *Serjania*, *Allophylus*, *Talisia*, *Cupania* and *Matayba* are the only important genera in terms of numbers of species. *Paullinia* and *Serjania* are by far the largest and perhaps the most complex genera in the family. *Serjania* is a genus usually inhabiting weedy areas and forest edges. Consequently, it has been better collected. *Paullinia*, on the other hand, commonly occurs in forests. Because many good forest habitats are being opened to collectors many new species of *Paullinia* will continue to be discovered. Panama appears to be richer than other parts of Central America in numbers of species for the family.

The sapindaceous flower (see *Serjania atrolineata*; Fig. 12) may be irregular, and if so, usually only 4 petals are present. In these cases the staminal cluster and the pistil occupy essentially opposite sides of the disc, the petals nearest the staminal cluster are frequently enlarged and are termed anterior petals, the other two petals are lateral petals. The petals all bear complex scales from near the base, and at least the anterior petals are borne on or are subtended by a swollen disc gland. The scales are thin and expanded in the basal portion and bear a thickened, often colored, frequently bilobed crest at the apex. The apical portion of the scale proper (basal portion) bears a decurrent appendage. The lateral margins of the basal portion of the scale are usually curved inward to form additional protection for the nectar which accumulates around the base of the petals. Since it has not been possible to readily determine whether stamens are functional, all flowers bearing well-developed stamens and pistils are here called bisexual. They may indeed all be functionally pistillate. Staminate flowers are more easily identified, as the pistil in these flowers is very much aborted.

Paullinia and *Serjania* are sometimes impossible to distinguish vegetatively, as are *Cupania* and *Matayba* (see discussion following these genera). Some explanation of leaf shape is warranted for certain genera. Biternate leaves of *Serjania* and *Paullinia* are compound leaves with 3 sets of 3 leaflets (see *Serjania atrolineata*; Fig. 12). Ternate-pinnate leaves found on *Paullinia* are compound leaves which have one or more sets of ternate leaflets at and/or near the base of the leaf, the remainder being merely pinnate.

The term "cataphyll" as used in *Talisia princeps* is not directly analogous to cataphyll as used in other families such as Araceae where the structure has evolved to form protection for new leaves. It does however qualify as a cataphyll, i.e., an early leaf form of a plant.

The vein axils of the lower leaf surface of a number of sapindaceous species bear domatia. The domatia may vary from distinctly foveolate to web shaped, being open only on the upper edge. The term as used here gives no assurance that they are actually inhabited by insects. In other species the vein axils are merely densely pubescent and are described as barbate or tufted.

In addition to the three cultivated genera, *Blighia*, *Filicium*, and *Melicoccus*, included in this treatment, one additional sapindaceous genus should be mentioned. The lychee, *Litchi chinensis* Sonn., might be expected in Panama though no specimens of it are known presently.

The family has no important uses though *Sapindus* fruits have been used for

soap and many species have been used as a "barbasco" or fish poison, thus the frequency of that common name in the family.

Literature:

Adams, C. D. 1972. Flowering Plants of Jamaica. University of West Indies, Mona, Jamaica.

Duke, J. A. 1968. Darien Ethnobotanical Dictionary. Batelle Memorial Institute, Columbus, Ohio.

Radlkofer, L. 1933–1934. Sapindaceae. *In* A. Engler (editor), Das Pflanzenreich. IV. 165 (Heft 98 a–h).

Standley, P. C. 1928. Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. 27: 1–416.

——— & J. A. Steyermark. 1949. Sapindaceae. *In* Flora of Guatemala. Fieldiana, Bot. (Part 6)24: 234–273.

a. Plants scandent, bearing tendrils.
  b. Fruit a samara, usually 3 together, with terminal or basal wings.
    c. Seed-bearing part of fruit positioned at apex of samara; leaves with 3–many leaflets; flowers slightly irregular ..... 13. *Serjania*
    cc. Seed-bearing part of fruit positioned at base of samara; leaves with 3 leaflets; flowers regular ..... 15. *Thinouia*
  bb. Fruit not a samara, often alate dorsally.
    d. Fruit a thick-walled capsule; seeds subtended by an aril; stems ligneous even above ..... 10. *Paullinia*
    dd. Fruit membranous; seeds never arillate; stems herbaceous above.
      e. Leaves biternate (with 3 sets of 3 leaflets); fruits inflated ..... 3. *Cardiospermum*
      ee. Leaves 3-foliolate; fruits never inflated ..... 16. *Urvillea*
aa. Plants erect, never bearing tendrils.
  f. Leaves simple ..... 6. *Dodonaea*
  ff. Leaves compound.
    g. Leaves bipinnate, with numerous, small leaflets ..... 5. *Dipterodendron*
    gg. Leaves once-pinnate, sometimes with only 2 or 3 leaflets.
      h. Leaves 3-foliolate with a terminal leaflet; sepals 4; persistent style eccentric on the fruit ..... 1. *Allophylus*
      hh. Leaves with several leaflets, usually without a terminal leaflet; sepals or calyx lobes usually 5; persistent style terminal or subterminal on the fruit.
        i. Fruit dehiscent, capsular.
          j. Stamens long exserted; fruit usually 5 cm long or longer; cultivated trees ..... 2. *Blighia*
          jj. Stamens little if at all exserted or less than 4 mm long; fruit less than 3 cm long; native trees.
            k. Capsule usually 2-lobed, deeply lobed to about half its length, glabrous outside; seed not arillate; petals lacking scales on inner surface; embryo incumbent, notorrhizal (the radicle positioned against the back of one of the cotyledons, the cotyledons thus incumbent) ..... 11. *Pseudima*
            kk. Capsule usually 3-lobed (2-lobed in *Cupania livida* and *Matayba ingaefolia* but densely pubescent outside), rounded to emarginate at apex, not deeply lobed; seed usually enveloped at base by a fleshy white aril; petals with scales on inner surface; embryo accumbent, pleurorhizal (the radicle positioned against one edge of the cotyledon, the cotyledons thus accumbent).
              l. Sepals distinct; blades usually markedly toothed and often conspicuously pubescent ..... 4. *Cupania*

ll. Sepals united; blades usually entire and glabrous or nearly so ..... 8. *Matayba*

ii. Fruit indehiscent, dry or fleshy.

m. Fruit distinctly 2- or 3-lobed, one or more of the lobes very small, representing an abortive cell; anthers versatile .. 12. *Sapindus*

mm. Fruit usually not lobed; anthers basifixed.

n. Leaf rachis distinctly winged ..... 7. *Filicium*

nn. Leaf rachis not winged.

o. Leaves usually with more than 4 pairs of leaflets (as few as 5 leaflets in *T. hexaphylla*); seeds ellipsoid; slender shrubs; native species ..... 14. *Talisia*

oo. Leaves usually with 2 pairs of leaflets; seeds globose; trees with stout trunks; cultivated species .. 9. *Melicoccus*

1. ALLOPHYLUS

Allophylus L., Sp. Pl. 348. 1753; Gen. Pl., ed. 5. 164. 1754. TYPE: *A. zeylanicus* L.

Cominia P. Browne, Civ. Nat. Hist. Jam. 205. 1756. TYPE: Based on *Rhus cominia* L. = *Allophylus cominia* (L.) Swartz.

Schmidelia L., Mant. Pl. 1: 10. 1767. TYPE: *S. racemosa* L. = *Allophylus racemosus* (L.) Radlk.

Usubis Burm.f., Fl. Ind. 81, *tab.* 32. 1768. TYPE: *U. triphylla* Burm.f. = *Allophylus racemosus* Radlk.

Aporetica J. R. & G. Forst., Char. Gen. Pl. 131, *tab.* 66. 1776. TYPE: *Aporetica ternata* J. R. & G. Forst. = *Allophyllus ternatus* (Forst.) Radlk.

Toxicodendron Gaertn., Fruct. 1: 207, *tab.* 44. 1788, non Tourn., nec Thunb. TYPE: *T. cobbe* (L.) Gaertner = *Allophylus cobbe* (L.) Blume.

Ornitrophe Comm. ex A. L. Juss., Gen. Pl. 247. 1789. TYPE: *O. borbonica* Gmel. = *Allophylus integrifolius* Blume.

Gemella Loureiro, Fl. Cochinch. 2: 648. 1790. TYPE: *G. trifolia* Loureiro = *Schmidelia gemella* Cambess.

Nassavia Vell., Fl. Flum. 1: 140. 1825. TYPE: *N. axillaris* Vell. = *Allophylus puberulus* Radlk.

Azzamara Hochst. ex Hochst., Linnaea 26: 79. 1843. TYPE: *A. trifoliata* Hochst. = *Allophylus abyssinicus* (Hochst.) Radlk.

Polygamous *shrubs* or small *trees*. *Leaves* (1–)3(–5)-foliolate, petiolate, exstipulate; leaflets entire or serrate, often punctate or lineolate. *Inflorescences* axillary, racemiform or loosely paniculate. *Flowers* irregular, small, pedicellate, globose or often closed at anthesis; sepals 4, imbricate, in opposite pairs, the other two smaller, cucullate, membranous, glabrate or barbate within; petals 4, spatulate, the petal scale short, bifid or V-shaped; disc unilateral, lobate or with 4 obtuse glands; stamens 8, eccentric; ovary eccentric, usually of 2 cells, bilobed, the style 2- or 3-lobate, eccentric in fruit, the ovules solitary, ascending from the base of the cell. *Fruit* a single (rarely 2) obovoid-globular, indehiscent, dry or fleshy coccus; seed obovoid with a short aril.

The genus contains about 190 species. Radlkofer's (1933–1934) monograph included 53 species for the Americas. Most of these are South American. Central America (including Mexico and Panama) has about 6 species with 3 in Mexico, 4 species in Middle America and 3 species in Panama. Both *Allophylus occidentalis* and *A. psilospermus* are known throughout the region. *Allophylus* differs from other Sapindaceae in Panama by being arborescent with 3-foliolate leaves.

Some West Indian species are unifoliolate but all Central American species are 3-foliolate.

a. Leaf blades densely and conspicuously pubescent between the veins on the lower surface ..... 2. *A. occidentalis*
aa. Leaf blades glabrous or nearly so between the veins on the lower surface.
  b. Inflorescence a simple raceme or with only short branches; leaf blades usually with tufts of trichomes in the axils of the lateral veins on the lower surface, drying green; dried fruits less than 7 mm long ..... 3. *A. psilospermus*
  bb. Inflorescence widely branched; leaf blades usually glabrous, lacking axillary tufts, drying brown; dried fruits more than 1 cm long ..... 1. *A. gentryi*

1. **Allophylus gentryi** Croat.[4] TYPE: Panama, *Dwyer & Kirkbride 7821* (MO-2258506, holotype; F, NY, PMA, US, USF, isotypes).

Trees to ca. 10 m tall; stems terete, prominently lenticellate, glabrous. *Leaves* 3-foliolate, 3–20 cm long; petiole obscurely sulcate, 1.5–2.8 cm long; petiolules 6–13 mm long, flattened on the upper surface with marginal ribs; leaflets oblong-elliptic, gradually acuminate, acute to attenuate at base, 8–18.5 cm long, 2.5–7 cm wide, glabrous or with some pubescence on the midrib and with occasional short tufts in the vein axils beneath, drying brown, the nerves 7–12 pairs, arcuate-ascending and extending to the margin, the margin thickened, minutely revolute. *Inflorescences* paniculate from the upper leaf axils, to ca. 12 cm long; rachis weakly tomentose; pedicels to 2 mm long (to 3 mm long in fruit), glabrate, articulate near the base. *Flowers* with sepals orbicular, ca. 1.5 mm long, appressed-puberulent on both surfaces especially within near the base; petals not seen; disc villous, the glands prominent, flattened laterally, sparsely pubescent; bisexual flowers with the ovary and style together 1.5 mm long, the stamens 1 mm long, densely villous to the middle, the ovary 2-lobed, weakly pubescent, the style branched in upper ½–⅓, the stigmas 2; staminate flowers not seen. *Fruits* composed of 1 or frequently 2 cocci, each obovoid, rounded at the apex, abruptly tapered to the base, 10–14 mm long, 6–9 mm wide, the pericarp thick, glabrous, drying brown, with longitudinally oriented sculpturing.

The species is named in honor of one of its collectors, Alwyn H. Gentry. It is distinguished from others in Panama by its large fruits. It is close to *Allophylus jamaicensis* Radlk. of Jamaica which differs in having fruits less than 1 cm long, in having longer petioles (usually 5–10 cm long), and in having a glabrous disc. It is also close to *A. robustus* Radlk. of the Guianas which has large fruits but thinner leaves and fruits that are conspicuously pubescent (at least when young).

Flowers of *A. gentryi* are known from August and mature fruits have been collected in January. The species is thus phenologically distinct from the other two Panamanian species which flower in the dry season and fruit in the rainy season.

Allophylus gentryi is known only from Panama. It occurs at about 1,000 m in tropical wet or premontane wet forest.

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[4] *Allophylus gentryi* Croat, sp. nov. Arbor circa 10 m alta. Folia trifoliolata; petiolus 1.5–2.8 cm longus. Inflorescentiae paniculate, ad circa 12 cm longae. Flores sepalis orbicularibus disco villoso glandibus prominentibus sparsim pubescentibus. Fructus unicoccis aut bicoccis, uterque obovatus, 1–14 mm longus, 6–9 mm latus, glaber.

DARIÉN: Cerro Pirre, *Bristan 1233* (NY). PANAMÁ: Cerro Jefe, to 3100 ft, *Dwyer & Gentry 9518* (MO, SCZ, NY). Cerro Campana, 3000 ft, *Dwyer & Kirkbride 7821* (F, MO, NY, PMA, US, USF); 2700 ft, *Wilbur & Weaver 11302* (DUKE).

2. **Allophylus occidentalis** (Swartz) Radlk., Sitzunsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20: 230. 1890.—FIG. 1.

A. racemosus Swartz, Prodr. Veg. Ind. Occ. 62. 1788, non. L. TYPE: Hispanola, *Swartz* (BM).
Schmidelia occidentalis Swartz, Fl. Ind. Occ. 2:665. 1800(1798), based on *Allophylus racemosus* Swartz.
Ornitrophe occidentalis (Swartz) Willd., Sp. Pl. 2(1): 323. 1799. TYPE: not seen.
Schmidelia unguicularis Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1): 399. 1858. TYPE: Cuba, Prov. St. Jago, Sierra Maestra, 2500 ft, *Linden 1701* (not seen).
S. velutina Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1): 400. 1858. TYPE: Guyana, *Schomburgk 741* (K, L, U).
Allophylus velutinus Radlk., Sitsungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20:314. 1890, nom. nud. TYPE: not seen.

Shrubs or small *trees* to 10 m high; stems slender, tomentose when young, glabrescent. *Leaves* 3-foliolate; petioles 2–6 cm long, flattened on the upper surface; leaflets elliptic to ovate to rhombic-lanceolate, acute to acuminate at the apex, acute to attenuate at the base, 5–25 cm long, 3–7 cm wide, repand-dentate, glabrate or inconspicuously pubescent between the veins above, the veins tomentose, with soft spreading trichomes beneath. *Thyrses* simple, about as long as the petioles. *Flowers* white to yellow; sepals orbicular to obovate, 1–1.5 mm long, ciliate, puberulent outside, glabrous inside; petals obovate, to 1.5 mm long, ciliate, the scale V-shaped, extending to about the middle of the petal, densely hispid; staminate flowers with stamens ca. 2.5 mm long, the filaments pubescent at the base, the ovary didynamous, pubescent; bisexual flowers with the styles pubescent, to 3 mm long, the stigmas 3, ca. 1 mm long, the stamens to 1.5 mm long, glabrous. *Fruits* of 2 obovoid cocci (1 usually aborting), to ca. 6 mm long, red, sparsely pubescent; seed obovoid, arachnoid-pubescent, to 4 mm long.

The species is similar to *Allophylus psilospermus* Radlk. except for being much more pubescent. Flowering is precocious, occurring mostly when the tree is putting on new leaves in the late dry and early rainy season from February to May. Fruits mature between March and August, especially June and July.

Allophylus occidentalis ranges from Guatemala and Belize to the West Indies, Panama, and northern South America. In Panama it is known from tropical dry forest and premontane wet forest but mostly from drier parts of tropical moist forest on the Pacific slope. No collections have been seen from the Atlantic slope of Panama.

CANAL ZONE: Juan Mina, *Bartlett & Lasser 16320* (MICH, MO). Road K-10, *Duke 11700* (NY). Madden Dam area, *Porter et al. 4057* (MO). Ancón Hill, *Standley 26379* (MO, US). Between Fort Clayton and Corozal, *Standley 29134* (US). Chiva Chiva Trail near Miraflores Lake, *Tyson & Blum 4012* (MO, SCZ). Curundu Survival School, *Tyson & Dwyer 4465* (GH, MO, SCZ). CHIRIQUÍ: Trail from San Félix to Cerro Flor, 100–850 m, *Allen 1924* (MO). East of Gualaca, *Allen 5036* (G, MO, US). 2 mi SW of Guabala, *Dwyer 4246* (SCZ). Tolé, *Dwyer & Kirkbride 7454* (US). Vicinity of David, 30–80 m, *Pittier 2840* (NY). 2 mi SW of Guabala *Tyson et al. 4246* (MO, SCZ). COCLÉ: Vic. of El Valle, *Bartlett & Lesser 16670* (MO). Penonomé, *Dwyer 2013* (MO). Between Las Margaritas and El Valle, *Woodson et al. 1301* (A, F, MO, NY). DARIÉN: Vic. of Piñas, *Duke 10596* (MO). Cuipo forests near Santa Fe, *Duke*

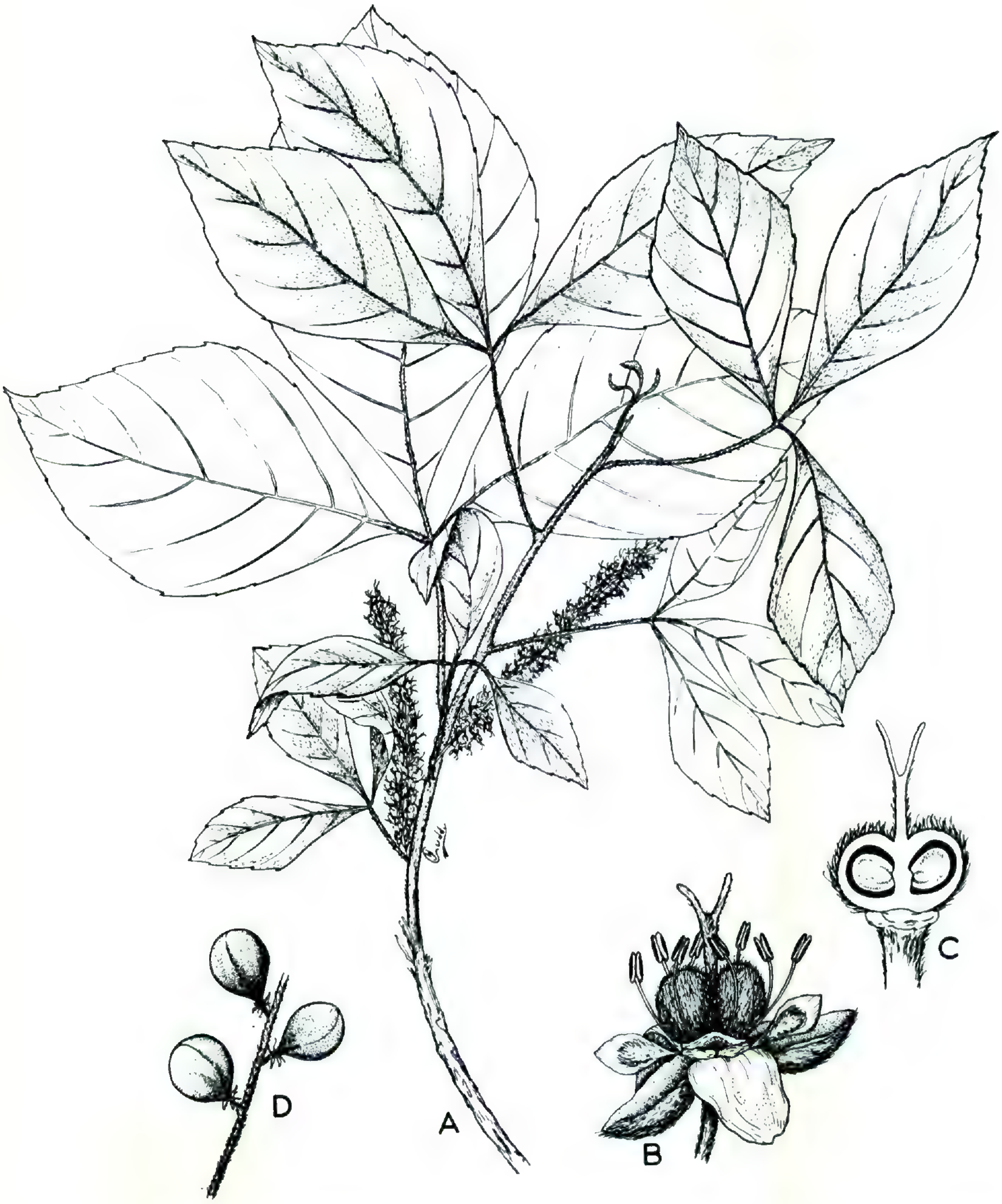

FIGURE 1. *Allophylus occidentalis* Swartz.—A. Flowering branch (× ½). [After *Williams & Molina 10612* (MO), Honduras.]—B. Bisexual flower (× 10½).—C. Pistil (× 12⁷⁄₁₀). [After *Smith 124* (MO), Costa Rica.]—D. Fruits (× 1⅗). [After *Allen 5036* (MO).]

12261 (MO). Trail from Río Pucro to Quebrada Maskia, *Duke 13059* (MO, NY). HERRERA: Alrededores de Ocú, *Carmen Díaz 50* (DUKE, MO, PMA). Road between Las Minas and Pesé, *Duke 12322* (MO). 12.5 mi S of Ocú, *Lewis et al. 1664* (GH, MO, US). PANAMA: Trapiche, Perlas Islands, *Allen 2629* (MO). Vic. of La Jagua, E of Panama City, *Bartlett & Lasser 16374* (MO). Vic. of Macambo, *Croat 14907* (F, MO). San José Island, *Duke 12538* (MO); *Erlanson 98, 154, 231, 372* (all US), *98, 231, 372, 387* (all GH); *Johnston 1258* (GH). Near Río Tapia, Juan Díaz Region, *Maxon & Harvey* (US). Between Río Pacora and Chepo, *Porter et al. 5163* (MO). Río Tapia, *Standley 26202* (US). East of Río Tocumen, *Standley 26535* (US). Río Tapia, *Standley 28111* (US). Near Matías Hernández, *Standley 28944* (US). Río Tocumen, *Standley 29486* (US). Tumba Muerta Road near Panamá, *Standley 29826* (US).

Juan Díaz, *Standley 30519* (US). Between Las Sabanas and Matías Hernández, *Standley 31886* (US). 1 mi W Tocumen, *Tyson & Blum 4102* (MO, PMA, SCZ). Cañita, 18 mi E of Chepo, *Tyson & Smith 4150* (MO, SCZ). Carretera Tumba María cerca Santa María, *Vargas 29* (MO, PMA). VERAGUAS: San Francisco, *Dwyer 1286* (DUKE, GH, MO). Tuté, *Dwyer 4299* (MO). Without exact locality, *Seemann 1212* (K). Vic. of Santiago, *Stern et al. 994* (MO, US). 5 m SE of Calobre, *Wilbur et al. 12143* (DUKE, F, GH).

3. **Allophylus psilospermus** Radlk., Sitzunsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20: 330. 1890. TYPE: Martinique, *Hahn 1175* (G, K, US).

A. panamensis Radlk., Sitzunsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 38: 212. 1908. TYPE: Panama, *Wagner* (M, L).

Slender *tree*, usually 5–10(–20) m tall; stems terete, glabrous except when young. *Leaves* 3-foliolate; petioles somewhat flattened laterally, 2–5(–7) cm long, strigose; leaflets elliptic to oblong-elliptic or oblanceolate, subsessile, acuminate at the apex, acute and sometimes inequilateral at the base, 2.5–26 cm long, 1.5–7.5 cm wide, remotely serrate, glabrate except for the sparsely pubescent veins and sometimes the tufts of trichomes in the axils of veins beneath. *Thyrses* puberulent, simple or paniculate, chiefly axillary. *Flowers* campanulate, cream or greenish white, ca. 2 mm wide, pedicellate; sepals ciliolate, orbicular to obovate; petals obovate, 1–2 mm long, glabrous, ciliolate, their scales united with petals to near the apex, densely villous, each subtended by a yellowish basal gland; staminate flowers with stamens well exserted, to ca. 2.3 mm long, clustered on one side of the flower, the filaments villous at least near the base, the pistillode obscure; bisexual flowers with the stamens less than 1 mm long, included, the ovary 2-celled, minutely hispidulous, the style borne between the 2 cells, 1.5–2 mm long, persisting in fruit but very oblique, held at base of fruit, the stigmas 2, recurved, densely papillate. *Fruit* of 2 obovoid cocci (1 usually aborting), 6–9 mm long, yellow to orange, finally red and glabrate at maturity with a thin fleshy pericarp covering the seed; seed 2–3 mm diam.

The species can be distinguished by its 3-foliolate leaves with the blades glabrate beneath except for the densely barbulate vein axils.

Flowering occurs in the dry season from January to May. The species may flower somewhat precociously or with fully developed leaves. Fruits mature in the early rainy season from May to August.

Allophylus psilospermus ranges from Mexico to Panama and the West Indies. The species is ecologically variable, occurring in tropical dry, premontane moist, tropical wet, premontane wet and tropical wet forests. In Panama it is most common in wetter parts of tropical wet forest and, unlike *A. occidentalis*, it occurs on the Atlantic slope of Panama.

CANAL ZONE: Barro Colorado Island, *Aviles 5* (F); *Bailey & Bailey 29* (F); *Croat 4978* (DUKE, F, MO, SCZ), *5031* (MO, SCZ), *5862* (DUKE, F, MO, NY, SCZ), *8781* (MO), *10155* (DUKE, F, MO, NY, SCZ), *10754* (F, MO, NY, SCZ), *14820* (MO, SCZ), *14823*, *15072* (both MO); *Dare 928* (MO); *Foster 538* (DUKE), *836*, *1009* (both DUKE, F, MO, PMA), *1498* (DUKE); *Oppenheimer 67-6-4-1420* (MO); *Standley 41012*, *41093* (both US); Zetek *3875* (F, MO, US). Pipeline Road, *Luteyn & Kennedy 4136* (DUKE). Along Caño Quebrada, *Pittier 6656* (US). Near Gatún, *Standley 27217* (MO, US). CHIRIQUÍ: Pozos de Salud at edge of Tolé, *Correa 129* (MO, SCZ). 32 mi W of Santiago, *Croat 10716* (MO, NY, SCZ).

Tolé, *Dwyer & Kirkbride 7454* (K, MO). Vic. of David, 30–80 m, *Pittier 2840* (US). Without exact locality, *Wagner s.n.* (M, L). Between Remedios and David, *White 307* (F, MO). COCLÉ: El Valle, 1000 m, *Allen 3419* (MO). SW of Cerro Pilón, ca. 900 m, *Croat 22915* (MO). Pocrí, *Dwyer 1199* (MO). Cerro Pilón, *Lallathin 14-4* (MO). Above El Valle de Antón, *Maxwell 4608* (SCZ). Cerro Pilón, 5 km NE of El Valle, 800–1045 m, *Mori 6597* (L, MO, PMA, S, TEX, VEN). Foot of Cerro Pilón, *Porter et al. 4608* (DUKE, MO, SCZ). Between Las Margaritas and El Valle, *Woodson et al. 1299* (F, MO, NY). DARIÉN: Río Ucurgantí, *Bristan 1125* (MO). Río Pucro, below village of Pucro, *Duke 13168* (MO). Confluence of Río Chucanaque and Río Canclones, *Duke 5123* (MO). LOS SANTOS: Pedasí, *Dwyer 2493* (MO). Punta Mala, *Tyson 2736* (MO, SCZ). PANAMÁ: Vic. of Finca Neptuno, 600–800 m, *Nee 11544* (MO, PMA). VERAGUAS: Río de Jesus, Río Trinidad, *Dwyer 1318* (MO). Los Toretos, *Dwyer 2447* (MO, US). 5 mi E of Santiago, *Tyson et al. 4283* (MO, SCZ). 5 mi SE of Calobre, *Wilbur et al. 12142* (DUKE, GH, MO).

2. BLIGHIA

Blighia Koenig, Ann. Bot. (König & Sims) 2: 571, *tab. 16–17*. 1806. TYPE: *B. sapida* Koenig.

Large, polygamous *trees*. *Leaves* sparse, exstipulate, petiolate, paripinnate; leaflets entire, pinnately veined. *Inflorescences* axillary, racemiform, the bracteoles small, buds subconical. *Flowers* narrowly pedicellate; calyx 5-parted, the lobes ovate-lanceolate, narrowly imbricate; petals 5, linear-lanceolate, bearing scales within from near the base; disc swollen, somewhat 8-lobed; stamens 8, inserted within the disc; ovary 3-locular, 3-carpellate. *Fruit* 3-locular, large, trigonous-pyriform; seeds arillate.

The genus has 7 species native to Africa.

1. **Blighia sapida**[5] Koenig, Ann. Bot. (König & Sims) 2: 571, *tab. 16–17*. 1806. LECTOTYPE: Guinea (Africa), *Isert & Thonning 155* (C).

Trees 8–15(–50) m tall; stems yellowish-tomentose when young, only sparsely pubescent in age. *Leaves* paripinnate; petiolules 3–7 mm long; leaflets in (3–)4(–5) pairs, cuneate-obovate, elliptic or oblong, obtuse, rounded or short-acuminate at the apex, obtuse to acute at the base, 4–21 cm long, 2.5–8.5 cm wide, entire, glabrate above, villous beneath at least on the midrib. *Racemes* in terminal axils, simple or compound, tomentose throughout; pedicels 3–5 mm long. *Flowers* cream colored; calyx deeply 5(6)-lobed, the lobes narrowly ovate; petals ovate-oblong, 3.5–4.5 mm long, villous on both surfaces, ciliate; disc flattened, densely villous; stamens 8–10; ovary short stalked, densely rufous-pubescent; staminate flowers with stamens long exserted, 4–6 mm long, the filaments villous to near apex, the ovary to ca. 1 mm long; bisexual flowers with the stamens to ca. 3 mm long, the ovary ovoid, narrowly tapered to the style, the style and stigmas together to 7 mm long, equalling the ovary. *Capsules* oblong-obovate, obtusely 3-lobed, 6–10 cm long, yellowish to red; valves 3, fleshy, glabrate outside, densely woolly-pubescent inside; seeds usually 3, globose, to 1.8 cm diam., black, shiny, drying dark brown, borne on a fleshy white aril, the aril several times larger than the seed itself.

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[5] For extensive synonymy, see Radlkofer (1933–1934).

Blighia sapida has several common names. Most commonly it is called "huevo vegetal," "arbol de huevo," "seso vegetal," and "akee" (English). The species is native to West Africa but is widely cultivated in tropical regions. In Panama it is not common except in regions populated originally by West Indians. The large fleshy aril is fried and eaten. At least prior to opening of the capsule, the aril is said to be poisonous.

BOCAS DEL TORO: Airport at Bocas del Toro, *Croat & Porter 16315* (MO). CANAL ZONE: U.S. Government Experiment Plantation, Frijoles, *Greenman & Greenman 5154* (MO). 3 km SE of Gamboa, *Nee 10851* (CAS, DUKE, F, GH, MO, NY, PMA), *11491* (CAS, DUKE, F, MO, NY, PMA). 9 km NW of Gamboa, 120–150 m, *Nee & Berg 8814* (CAS, COL, DUKE, GH, K, MO, NY, P, PMA, RSA, TEX, US, VEN). Between Gorgona and Mamé, 10–30 m, *Pittier 2238* (NY, US). Frijoles, *Standley 27662* (US). Around Balboa, *Standley 30907* (US).

3. CARDIOSPERMUM

Cardiospermum L., Sp. Pl. 366. 1753; Gen. Pl., ed. 5. 171. 1754. TYPE: *C. halicacabum* L.

Corindum Miller, Gard. Dict., abr. ed. 4. 1754, non Adanson. TYPE: *C. halicacabum* (L.) Miller = *Cardiospermum halicacabum* L.

Rhodiola Loureiro, Fl. Chochinch. 627. 1790. TYPE: *R. biternata* Loureiro = *Cardiospermum halicacabum* L.

Polygamous, herbaceous, annual or perennial *vines*; stems herbaceous to woody with axillary or peduncular tendrils. *Leaves* usually biternate, occasionally decompound or with a lesser number of leaflets, hispid to glabrous, often with pellucid dots or lines; stipules small, rarely wanting. *Inflorescences* axillary panicles. *Flowers* irregular; sepals 5, often with 2 sepals entirely connate, the outer 2 much smaller; petals 4, the scale on the inside of the petal with a bilobed crest and a deflexed barbate appendage; disc glands 4, the 2 superior ovate or cornute, the 2 inferior obsolete; stamens 8, eccentric, the filaments unequal, free or connate at the base; ovary trilocular, triquetrous, sessile or stipitate, the style filiform, the stigmas 3, the ovule solitary. *Fruits* capsular, 3-celled, inflated, obovate, subglobose or turbinate, membranous or subchartaceous; seed globose, the funicle round, reniform or cordate, the embryo curved, the radicle short, the inner cotyledon plicate.

The genus has about 14 species, but it is in need of intensive study and probably contains fewer species than are presently recognized. Two species are now known from Panama and at least one other from Central America. *Cardiospermum halicacabum* is included here because it is expected to be found in Panama.

a. Fruits generally 5–6 cm long, glabrous, longer than broad; flowers mostly 8–10 mm long; glands of the disc in part elongate and hornlike ..... 1. *C. grandiflorum*
aa. Fruits mostly 1–4 cm long, usually pubescent, broader than long or as long as broad; flowers 1.5–5 mm long; glands of the disc short, suborbicular or obsolete.
  b. Fruits suborbicular, as long as broad, 2–4 cm long; flowers 3–5 mm long ..... 2. *C. halicacabum*
  bb. Fruits broader than long, 1–3 cm long; flowers 2–3 mm long ..... 3. *C. microcarpum*

1. **Cardiospermum grandiflorum** Swartz, Prodr. Veg. Ind. Occ. 64. 1788. TYPE: Jamaica, *Swartz 4726* (US).

C. hirsutum Willd., Sp. Pl. 2(1): 467. 1799. TYPE: Guinea (not seen).
C. vesicarium Humb., Rel. Hist., Voyage 1:39. 1814. TYPE: not seen.
C. elegans H.B.K., Nov. Gen. Sp. Pl. 5:99, *tab. 439*. 1821. TYPE: Peru, *Humboldt & Bonpland* (P).
C. coluteoides H.B.K., Nov. Gen. Sp. Pl. 5:101. 1821. TYPE: Brazil, *Humboldt & Bonpland* (P).
C. macrophyllum H.B.K., Nov. Gen. Sp. Pl. 5:108. 1821. TYPE: Venezuela, Mission del Orinoco, prope Atures, *Humboldt & Bonpland* (P).
C. inflatum Vell., Fl. Flum. 1:150, *pl. 22*. 1825. TYPE: Brazil (plate seen).
C. pilosum Vell., Fl. Flum. 1:151, *pl. 26*. 1825. TYPE: Brazil, oppidum Pharmacopolis (plate seen).
C. duarteanum Cambess. in St.-Hilare, Fl. Bras. Mer. 1:271. 1828. TYPE: Brazil, Minas Gerais, prope Contendas (not seen).
C. velutinum Hook & Arn., Bot. Misc. 3:158. 1833. TYPE: Uruguay, *Tweedie* (K).
C. barbicule Baker in Oliv., Fl. Trop. Afr. 1:418. 1868. TYPE: Cameroon, *Mann* (not seen).

Robust herbaceous *vines*; stems 5- or 6-ribbed, pubescent or glabrate. *Leaves* biternate; petioles terete, 2–5 cm long; leaflets ovate or oblong to obovate, acuminate or obtuse, attenuate at the base, broadly serrate or incised-dentate, membranous, 5–8 cm long, 2–3.5(4) cm wide, sparsely pubescent to subglabrous; stipules subulate, small. *Thyrses* long-pedunculate on a tendril; pedicels 4–6 mm long. *Flowers* white; sepals 4, the 2 outer small, ovate, hispid, the 2 inner oblong, 6–8 mm long, glabrous; petals glabrous, obovate, attenuate, equal to the sepals, the scale on the inside of the petal oblong-obovate, 4–5.5 mm long, glabrous, with a lateral fold running the full length of the margin, the crest emarginate, the deflexed appendage slender, villous at the apex, extending nearly or all the way to the base of the flower; disc with 2 slender, elongate, corniform glands, 2–3.5 mm long; staminate flowers with stamens to 8 mm long, united into a tube in the lower half, the tube weakly pubescent, the ovary borne within the staminal tube on a stipe to 1.5 mm long, elliptic, glabrous, the styles 3, the ovary, styles and stipe together to 3 mm long; bisexual flowers with the stamens to 4 mm long, glabrous, the filaments not united at the base, the ovary and style together to 6 mm long, the ovary 3-angled, oblong-elliptic, conspicuously hispid on the angles, the style 3 mm long, 3-branched in the upper half. *Fruits* elongate, obovate or elliptic capsules, membranous, inflated, acutely 3-angled, 5–6 cm long, acute at both ends, glabrous or nearly so; seeds globose, black, ca. 7 mm diam., the hilum round, conspicuous but much narrower than the body of the seed.

Cardiospermum grandiflorum is distinguished by its large flowers and fruits. This species is much less variable than most species of the genus. Flowering occurs principally in the early dry season with fruits maturing as early as January.

The species ranges throughout continental tropical America and tropical Africa. According to Adams (1972) it is sparsely scattered in the West Indies. The species is ecologically variable. In Panama it is known from tropical dry forest, premontane moist forest, tropical moist forest, and tropical wet forest at low and middle elevations.

BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2717* (MO, PMA), *2725* (MO). Changuinola to 5 mi S, *Lewis et al. 859* (GH, MO, US). CANAL ZONE: Near Tropical Survival

School, *Correa s.n.* (DUKE). Radar Station Road, *Croat 9093* (MO, SCZ). Near Tropical Survival School, *Gauger s.n.* (MO, PMA, SCZ). Fort Kobbe, *Gentry 2860* (MO). Cerro Galera, 350–400 m, *Gentry 6618* (DUKE, MO), *619* (MO). Without exact locality, *Greenman & Greenman 5163* (MO). Gamboa, *Greenman & Greenman 5169* (MO). Pedro Miguel, *Killip 3349* (US). Empire to Mandinga, *Piper 5527* (US). Between Gorgona and Mamei, 10–100 m, *Pittier 2245* (NY, US). K-9 Road, *Sharp* 13 Dec. 1962 (MO, SCZ). Road K-15 near Huille, *Smith et al. 3279.* Near Summit, *Standley 25818* (US). Balboa, *Standley 26056* (MO, US), *26064* (S, US). Corozal Road near Panamá, *Standley 26782* (US). Balboa, *Standley 27143* (US). Gamboa, *Standley 28311* (US). Balboa, *Standley 29283* (US), *29292* (US). Near Summit, *Standley 29535* (US). Obisbo, *Standley 31739* (US). Balboa-Gorgas Memorial Laboratory, *White & White 61* (A, MO, NY). Vic. of Miraflores Lake, *White 261* (MO, US). COCLÉ: El Valle, ca. 500 m, *Hunter & Allen 362* (G, GH, MO). El Valle, *Lewis et al. 2580* (MO, SCZ). Bismark above Penonomé, *Williams 274* (NY, US). COLÓN: Río Gatuncillo, vic. of Santa Rosa (MO). PANAMÁ: Taboga Island, *Allen 93* (F), *1666* (GH, MO, US). Chepo, *Carrasquilla & Escobar 279* (MO, PMA); *Escobar et al. 279* (MO, PMA). Nuevo Granada, *Hayes 784* (NY). Sabanas near Chepo, 30 m, *Hunter & Allen 93* (G, MO, NY, US).. Cerro Campana, ca. 750 m, *Kennedy 2046* (DUKE, MO, PMA). Without exact locality, *Kennedy et al. 2079* (MO). Vera Cruz, *Lewis et al. 3002* (MO, SCZ). Panama City, *MacBride 2600* (F, G, US). Sabanas N of Panama City, *Paul s.n.* (US). Old Panama, *Porterfield s.n.* (NY). Arraiján Road, *Sharp* 11 Dec. 1962 (SCZ). Bella Vista, *Standley 25319* (GH, US). Taboga Island, *Standley 27111* (US). Juan Franco Race Track near Panamá, *Standley 27677* (US). Taboga Island, *Standley 27907* (US). Juan Díaz, *Standley 30559* (US). 4 mi E of Chepo, *Tyson 5358* (SCZ). VERAGUAS: 1–3 km above Escuela Agrícola de Alto Piedra, 700–800 m, *Croat 25984* (MO). 1–2 mi above Santa Fe, *Gentry 3042* (MO). 1–5 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 5330* (CAS, MO, PMA, TEX). WITHOUT EXACT LOCALITY: *Hayes 151* (US); *Kennedy 2287* (DUKE, MO, PMA).

2. **Cardiospermum halicacabum** L., Sp. Pl. 366. 1753. TYPE: Indies, Herb. Linn. 513.1 (LINN, not seen, MO, microfiche).

C. corindum L., Sp. Pl., ed. 2. 526. 1762. TYPE: Brazil (not seen).
Corindum halicacabum (L.) Medic., Malven-Fam. 110. 1787.
Cardiospermum glabrum Schum. & Thonn., Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh. 3:217. 1828. TYPE: Guianas, Sabalo incolis (not seen).
C. corycodes Kunze, Linnaea 17:579. 1843. TYPE: Cuba, *Doering* (not seen).
C. luridum Blume, Rumphia 3:184. 1847. TYPE: Java (not seen).

Annual *vines*; stems 5- or 6-ribbed, glabrous or minutely pubescent. *Leaves* biternate; leaflets oblong to ovate, obtuse or subacute at apex, attenuate or acute at the base, 2–8 cm long, 1–2.5 cm wide, deeply incised-dentate, membranous, pubescent or glabrate; stipules subulate, small. *Thyrses* long-pedunculate on a tendril, umbellike in appearance. *Flowers* yellowish white, mostly 4–5 mm long; sepals 4, the outer 2 small, pubescent, the inner 2 large, glabrous, oblong, ca. 4 mm long; petals obovate, attenuate, equal to the inner sepals, the scale round, to 2.5 mm long, the deflexed appendage oblong, villous especially along the margins, the crest obovate, orange; disc with 2 conspicuous suborbicular, glabrous glands 0.5 mm long; filaments pilose, those of the staminate flowers to 3.5 mm long. *Capsules* subglobose, 3-lobed, 3–4 cm long, membranous, inflated, pubescent, green to brown or reddish brown; seeds globose, black, 5 mm long, the hilum large, bilobed.

The species is found throughout the tropics and also enters into certain subtropical regions. Though no specimens are available from Panama, the species will probably be found there.

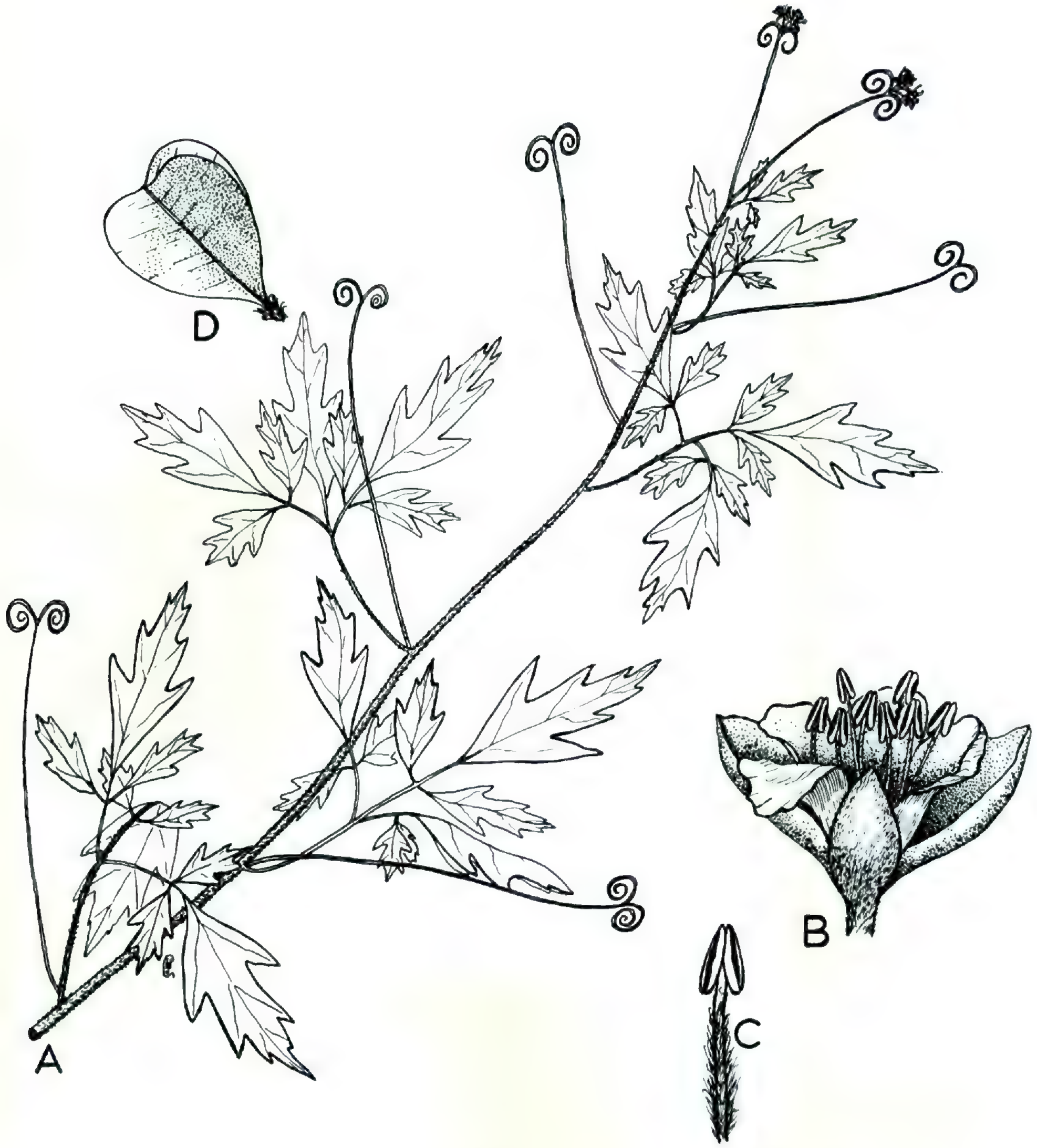

FIGURE 2. *Cardiospermum microcarpum* H.B.K.—A. Flowering branch (×7/10).—B. Staminate flower (×6 7/10).—C. Stamen (×8).—D. Fruit (×1 3/10). [After *Greenman & Greenman 5082* (MO).]

3. **Cardiospermum microcarpum** H.B.K., Nov. Gen. Sp. Pl. 5: 104. 1821. TYPE: Venezuela, Missiones del Orinoco, prope S. Fernando de Atabapo, *Humboldt & Bonpland 1184* (P).—FIG. 2.

C. acuminatum Miq., Linnaea 18:359. 1844. TYPE: Surinam, prope Paramaribo, *Miquel* (K).
C. pumilum Blume, Rumphia 3:184. 1847. TYPE: Seychelles Islands (not seen).
C. truncatum A. Rich., Tent. Fl. Abyss. 101. 1847. TYPE: Ethiopia, Prov. of Chire, *Dillon* (not seen).

Small herbaceous *vines*; stems 6-costate, glabrate. *Leaves* biternate; petioles terete, 0.5–4 cm long; leaflets oblong to lanceolate, obtuse or subacute at the apex,

attenuate-petiolate at the base, 1.5–4.5 cm long, 0.5–1.8 cm wide, deeply incised-dentate, membranous, rugulose, sparsely strigose especially on veins, the midrib sharply raised; stipules minute, scabrous. *Thyrses* long-pedunculate on a tendril, umbellike in appearance. *Flowers* white; sepals 4, the outer 2 small, rugulose, strigose, the inner 2 twice as large, rugulose, glabrous, obovate, 2.3 mm long, 2 mm wide, concave; petals obovate, 2–2.5 mm long, the anterior scales free or fused to about the middle of the petal, densely villous to glabrous except along the villous margins, the deflexed appendage deltoid, villous along the margin, the crest broadly obovate, as broad as long, the lateral petals with the scale sparsely villous to almost glabrous, the appendage lacking, the crest as in the anterior petals; disc with 2 broad glands; stamens 8, the filaments villous; bisexual flowers with the stamens to ca. 1 mm long, the ovary obcordate, 3-sided, densely villous, to 1.8 mm long, the style 3-lobed to about the middle, ca. 1 mm long; staminate flowers with the stamens to 3 mm long, the ovary nearly glabrous, 3-sided, the stigmas 3, about as long as ovary, together with the ovary ca. 1 mm long. *Capsules* inflated, obreniform, 3-lobed, 1 cm long, 2 cm broad, sparsely pubescent; seed globose, 4 mm long, black, shiny, the hilum obcordate, white.

Cardiospermum microcarpum is distinguished from other species of *Cardiospermum* by having a capsule broader than long. It was considered a variety of *C. halicacabum* L. by Radlkofer (1933–1934) and was included as a synonym of *C. halicacabum* by Standley & Steyermark (1949). Floral dissections lead me to believe that there are markedly different taxa going under the names *C. halicacabum* and *C. microcarpum*, and therefore, I have treated *C. microcarpum* as a distinct species. Few sheets have mature flowers to allow a thorough study of variation, but the few flowers studied were markedly variable.

Cardiospermum microcarpum is widely distributed in tropical areas. In Panama the species is known from disturbed areas in tropical dry forest, premontane moist forest, and drier parts of tropical moist forest. The species flowers and fruits principally in the dry season, December to April.

CANAL ZONE: Ancón Hill, *Greenman & Greenman 5082* (MO). Las Cruces Trail, 75 m, *Hunter & Allen 665* (MO). HERRERA: Road from La Avena to Pesé, *Burch et al. 1280* (GH, MO, NY). Vic. of Pesé, *Croat 9675* (MO, SCZ). PANAMÁ: Camino de Las Sabanas, *Herbierto* (US). Ca. 1 mi from Chepo, *Wilbur & Luteyn 11810* (DUKE, GH, MO). Chepo, ca. 60 m, *Pittier 4639* (US). Las Sabanas, *Standley 25858* (US).

4. CUPANIA

Cupania L., Sp. Pl. 200. 1753; Gen. Pl., ed. 5. 93. 1754. TYPE: *C. americana* L.

Trigonis Jacq., Enum. Pl. Carib. 3:19. 1760. TYPE: *T. tomentosa* Jacq. = *Cupania americana* L.

Trigonocarpus Vell., Fl. Flum. 1:153. 1825. TYPE: *T. racemosus* Vell. = *Cupania castanaefolia* Mart.

Polygamous *shrubs* or *trees* with terete, sulcate stems; young branchlets usually pubescent. *Leaves* even- or odd-pinnate; leaflets alternate or rarely subopposite, entire or dentate, often glabrous on the upper surface, glabrous or pubescent on

the lower surface, petiolate, exstipulate. *Inflorescences* paniculate or racemiform thyrses. *Flowers* small, regular; sepals 5, free, imbricate in two rows, orbicular, concave; petals 5, naked or with 1 or 2 scales within; disc annular and tumid, lobed, tomentose or glabrous; stamens usually 8, inserted within the disc, exserted in the staminate flowers, the filaments subulate-filiform, tomentose or glabrous; ovary 2–4-valvate, glabrous or pubescent outside, glabrous, tomentose or hispid inside. *Fruits* with seeds subglobose or oblong, arillate; embryo thick, curved, the cotyledons plano-convex, the radicle inflexed.

About 45 species are known for this genus, all in tropical America. *Cupania* is not always easily separable from *Matayba*. In addition to the key character given, i.e., sepals distinct for *Cupania* versus sepals united for *Matayba*, *Matayba* usually has a prominently stipitate fruit in comparison to *Cupania*. *Cupania guatemalensis* and *C. hirsuta* are most difficult to separate from *Matayba*.

a. Lower surfaces conspicuously pubescent, the trichomes either moderately long or the surface closely matted with shorter trichomes.
  b. Lower leaf surfaces usually white, the minute trichomes appressed and contiguous or nearly so; capsules subglobose, densely light brown tomentose ..... 1. *C. cinerea*
  bb. Lower leaf surfaces sparsely to densely reddish brown pubescent, the trichomes long and erect, not at all contiguous; capsules conspicuously 3-lobed, dark reddish brown hirsute or tomentose.
    c. Capsules with the wings extending forward, thus somewhat hornlike; leaf blades conspicuously serrate-dentate on the margins and narrowly acute at the base ..... 4. *C. hirsuta*
    cc. Capsules not as above, not at all hornlike; leaf blades entire, if not, then mostly obtuse to rounded at the base.
      d. Capsule lobes lacking narrowly winged margins; leaf blades mostly acute at the base ..... 3. *C. guatemalensis*
      dd. Capsule lobes with winged margins; leaf blades mostly obtuse to rounded at the base ..... 7. *C. rufescens*
aa. Lower leaf surfaces glabrous or inconspicuously pubescent to the naked eye (younger leaves of some species may appear pubescent).
  e. Capsule valves glabrous or only sparsely appressed-pubescent on the outer surface.
    f. Leaflets entire, glabrous beneath except in the pitlike, axillary domatia ..... 9b. *C. sylvatica* var. *fosteri*
    ff. Leaflets serrate-dentate, appressed-pubescent on the reticulate veins beneath ..... 2. *C. dukei*
  ee. Capsule valves densely and conspicuously tomentose.
    g. Capsules subglobose, the valves thick, to 3 mm thick in dried specimens ..... 5. *C. latifolia*
    gg. Capsules conspicuously lobed, the valves thin, usually less than 1 mm thick in dried specimens.
      h. Capsules 2-lobed, the valves dark reddish brown (indian red) tomentose ..... 6. *C. livida*
      hh. Capsules 3-lobed, the valves light reddish brown, red or bright red orange.
        i. Capsules red to red orange, truncate to subcordate at the base, usually lacking an evident stipe, each lobe bluntly emarginate at the apex, the capsule thus appearing 6-lobed; reticulate venation of the leaflets sparsely puberulent; axils of lower lateral veins lacking pitlike or weblike domatia ..... 9a. *C. sylvatica* var. *sylvatica*
        ii. Capsules reddish brown, acute to attenuate at the base, usually with a short stipe, the lobes acute to rounded at the apex, not appearing 6-lobed; reticulate venation of the leaflets glabrous, the axils of the lower lateral veins usually with pitlike or weblike domatia .. 8. *C. scrobiculata*

1. **Cupania cinerea** Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 38. 1844. TYPE: Peru, Maynas ad Yurimaguas, *Poeppig 2338* (F, NY, W).

C. costaricensis Radlk., Repert. Spec. Nov. Regni Veg. 17:364. 1921. TYPE: Costa Rica, *Tonduz* (B, destroyed, MO, photo).
C. alba Griseb., Bonplandia 6:4. 1858. TYPE: Colombia, Cauca Valley, Río Sucio, *Goudot* (P).

Trees to ca. 8(–10) m tall; stems terete, conspicuously lenticellate, often flexuose, young stems tomentose, glabrescent. *Leaves* pinnately 3–7-foliolate; petioles 1–6 cm long, tomentose to glabrescent; petiolules ca. 5 mm long; leaflets obovate, rounded to truncate or emarginate at the apex, acute at the base, 6–17 cm long, 3.5–7 cm wide, glabrate above, usually densely white-tomentose below, the pubescence all directed inward toward centers of the areoles, sometimes the lower surface dark, the pubescence moderately sparse on the reticulate veins, the actual surface then visible, the margins serrate-dentate to conspicuously serrate. *Panicles* dense, terminal or subterminal, racemose. *Flowers* white; sepals 5, ovate, tomentose, greenish; petals 5, ± obovate, to 2 mm long, clawed, villous, the blade laterally fused to the scale and deeply divided in the middle; stamens ca. 3 mm long, inserted on inner edge of the disc, the filaments villous below the middle; disc fleshy, ca. 0.7 mm high, tomentose; staminate flowers with the stamens exserted, 2.5–3 mm long, the ovary abortive, pubescent, lacking a style; bisexual flowers with the stamens 1.5–2 mm long, only slightly exserted, the ovary ovoid, obtusely 3-angulate, with a stout style about as long as the ovary, the style and ovary together ca. 3 mm long, the stigmas 3, recurved, the ovary, style and stigma tomentose. *Capsules* obovate, rounded to 3-lobed, short-stipitate, ca. 1.5 cm long and 1 cm wide, pale greenish- or brown-tomentose outside, woolly within; seeds oblong, more than 1 cm long, shiny black, the lower half covered with an orange aril.

Cupania cinerea is distinguished from other species in the genus in Panama by the dense mat of whitish pubescence on the lower leaf surface. Unusually dark-leaved specimens such as *White 259* with pubescence similar to *Cupania latifolia* may represent hybrids with that species.

Cupania cinerea flowers in the early rainy season in June and July. Fruits mature in September and October in Panama.

The species ranges from Costa Rica to Venezuela, Colombia, Peru, and Bolivia. It also occurs in the West Indies. In Panama it is known from tropical moist forest and tropical wet forest.

Common names are "gorgojo," "gorgojero," or "gorojo blanco."

BOCAS DEL TORO: Region of Almirante, *Cooper 351* (F, NY, US). Changuinola Valley, *Dunlap 507* (F, GH, US). Vic. of Chiriquí Lagoon, *von Wedel 2512* (GH, MO, NY, US), *2550* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 958* (F); *Croat 6440* (F, MO, NY, PMA, SCZ), *6696* (MO, NY, SCZ), *11767* (MO, NY); *Shattuck 958* (F, US); *Standley 40968* (US). Near Gamboa, *Bartlett & Lasser 16507A* (MICH, MO). Pipeline Road, *Clewell & Tyson 3263* (MO). Across from Summit Hills Golf Course, *Croat 10961* (F, MO, NY, SCZ), *12235* (DUKE, MO, NY, SCZ). Road S-10 N of Escobal, *Croat 12440* (DUKE, F, MO, NY, SCZ). Road K-6 E of Arraiján, *Croat 15038* (DUKE, F, GH, MO, NY). Forest N of Summit Hills Golf Course, *Croat 16652* (MO). 6 km W of Gamboa, 30–40 m, *Nee 7209* (CAS, DUKE, GH, K, MO, P, PMA, VEN). Gamboa, *Pittier 3704* (US). Vic. of Miraflores Lake, *White s.n.* (MO). COLÓN: Vic. Río Piedras, *Blum et al. 2534* (MO). María Chiquita, *Dwyer 1235* (MO).

Río Piedras along road to Portobelo, *Dwyer et al. 2534* (SCZ). Along Río Fató, *Pittier 3875* (US). DARIÉN: Río Pirre, 2–5 mi above El Real, *Duke 5092* (GH, MO, US). Río Pucro below village of Pucro, *Duke 13136* (MO). Vic. of Paya, Río Paya, *Stern et al. 188* (G, MO, US). Peñas Bay, *Tyson 5535* (DUKE, MO). PANAMÁ: Río Tapia, *Standley 28097* (US). Obisbo, *Standley 31753* (US).

2. **Cupania dukei** Croat.[6] TYPE: Panama, *Duke 8560* (MO-1832815, holotype).

Medium-sized *trees* to 15 cm d.b.h.; younger stems sulcate, densely appressed-puberulent, soon terete, glabrous, weakly shiny, densely covered with rows of whitish lenticels. *Leaves* pinnately compound, 4–7-foliolate; petioles 2.5–6 cm long; petiole and rachis glabrate to inconspicuously puberulent; petiolules ca. 5 mm long, swollen; leaflets oblong-obovate to oblong-elliptic, rounded to obtuse at the apex, inequilaterally attenuate at the base, one side to 1 cm above the petiole, 3–20 cm long, 1.5–7 cm wide, coarsely serrate, the teeth glandular, often curled inward, the upper surface glabrous, the lower surface sparsely to densely appressed-puberulent on the midrib and reticulate venation, the trichomes spreading toward the centers of the areoles, the upper surfaces of the reticulate venation glabrous or only sparsely pubescent, the reticulate veins prominulous. *Flowers* not known but inflorescence probably much like the closely related *C. cinerea*. *Fruits* deeply 3-lobed, to 12 mm long and 17 mm wide, truncate to obcordate at the apex, obtuse to truncate at the base, densely and minutely tuberculate, glabrate to appressed pubescent between the tubercles outside, sparsely woolly within and the surface visible, shiny; seeds 3, globose, shiny, ca. 5 mm diam., arillate at the base.

Cupania dukei is closely related to *C. cinerea* but is distinguished from that species by its deeply 3-lobed, glabrate fruits.

It occurs in premontane wet or tropical wet forests in Panama.

DARIÉN: Río Pirre near El Real, *Croat 15489* (MO, SCZ). Vic. of Caná, 1750 ft, *Stern et al. 473* (G, GH, MO, US). SAN BLAS: Río Chucunaque 2–10 mi above Cuna-Darién boundary, *Duke 8560* (MO).

3. **Cupania guatemalensis** (Turcz.) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9: 517. 1879.

Paullinia guatemalensis Turcz., Bull. Imp. Soc. Naturalistes Moscou 32:268. 1859. LECTOTYPE: Guatemala, *Friedrichsthal* (K).

Shrubs or small *trees* 3–10 m tall; stems terete, striated, yellow-tomentose when young, glabrate with age. *Leaves* pinnate; petiolules 3–7 mm long; leaflets 3–10, oblong-lanceolate to ovate, acute to oblong or oblanceolate at the apex, obliquely acute at the base, 5–20 cm long, 2–6.5 cm broad, the margin subentire to remotely denticulate, membranous, glabrous on the upper surface except for the villous veins, the lower surface velutinous, papillose. *Panicles* axillary or terminal, shorter than the leaves, 6–20 cm long, few branched; bracteoles subulate, tomen-

[6] *Cupania dukei* Croat, sp. nov. Arbor ad 15 cm diametrum. Folia 4–7-foliolata; petiolus 2.5–6 cm longus; foliola oblonga-obovata ad oblonga-elliptica, 3–20 cm longa, 1.5–7 cm lata, grosse serrata dentibus glandulosis. Flores ignoti. Fructus profunde trilobatus, ad 12 mm longus et 17 mm latus, dense minuteque tuberculatus; semina 3, globosa, nitida, basim arillata.

tose; pedicels to 1 mm long, thick, densely tomentose. *Flowers* white; sepals ovate, 3 mm long, thick, not imbricate at anthesis, tomentose outside, glabrate inside; petals long-unguiculate, obovate-cuneate, 2.3 mm long, the scale fused to the petal laterally, the margin and inner surface villous, the outside glabrous; disc glabrous outside, sparsely puberulous inside; filaments filiform, flattened, villous; bisexual flowers with stamens to 2 mm long, the ovary and style 3 mm long. *Capsules* turbinate, triquetrous, 3-lobed, ca. 1.5 cm long, short-stipitate, chartaceous, reddish-brown, densely and shortly pubescent outside, glandulose inside; seeds ellipsoid, ca. 1 cm long, shortly arillate.

Cupania guatemalensis may be confused with *C. rufescens* which is similarly pubescent, but that species has a fruit which bears a narrow wing around its margin. In addition it is usually a much larger tree than *C. guatemalensis*.

The species flowers in the dry season from January to April. Fruits mature in the late dry season and early rainy season beginning about April.

Cupania guatemalensis ranges from Mexico to Panama. In Panama it usually occurs in tropical moist and premontane wet forests and rarely in tropical wet forest.

COCLÉ: Mountains beyond La Pintada, *Hunter & Allen 629* (F, G, GH, MO, NY, U). El Valle, ca. 500 m, *Hunter & Allen 386* (GH, MO, NY, P). 2 mi S of Cerro Pilón, ca. 900 m, *Liesner 721* (CSA, MO, NY, PMA, US, VEN). Penonomé and vic., *Williams 336* (US). CHIRIQUÍ: Near Caldera on Chiriquicito-Caldera Trail, *Kirkbride & Duke 1004* (MO). Forests around Remedios, 0–30 m, *Pittier 3384* (M, NY, US). Remedios and vic., 0–100 m, *Pittier 5464* (US). Without exact locality, *Wagner s.n.* (M). DARIÉN: Río Pirre, *Duke 8294* (MO). HERRERA: 1 mi N of Macaracas on Río La Villa, *Tyson et al. 3142* (MO, SCZ). LOS SANTOS: Los Toretos, *Dwyer 2427* (MO). VERAGUAS: 2 mi S of Cañazas, *Tyson 3705* (MO, SCZ).

4. **Cupania hirsuta** Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9: 517. 1879. TYPE: British Guiana, *Schomburgk 277* (G, W).

C. cooperi Standley, Publ. Field Columbian Mus., Bot. Ser. 4:223. 1929. TYPE: Panama, *Cooper 543b* (BM, F, G, NY, US).

Trees to 12 m tall; stems sulcate, densely hirsute-tomentose when young, glabrescent. *Leaves* pinnate; leaflets 6–12, nearly sessile or with a petiolule to 3 mm long, elliptic-oblong to obovate-oblanceolate, acuminate at the apex, acute to attenuate at the base, 4–20(–28) cm long, 2.2–7(–11) cm wide, glabrous on the upper surface except hirsute on the major veins, hirsute throughout below, especially on the veins, the surface shiny, the margin serrate-dentate in the outer ⅔. *Inflorescences* terminal or upper axillary panicles to ca. 20 cm long, the branches, pedicels and calyces rufous-tomentose; bracteoles subulate, to 2 mm long; pedicels 1–1.5 mm long. *Flowers* white; sepals ovate-oblong, 2–3 mm long; petals obovate, to 2 mm long, glabrous on the outer surface except on the short claw, the scale fused to the lateral margin on the inner surface in the lower half, densely villous; bisexual flowers with the stamens 2.5–3 mm long, the filaments villous in the lower ⅔, the disc glabrous. *Capsules* turbinate-trilobed, subtricornute, ca. 1.5 cm long, reddish brown hirsute both inside and outside; seeds ellipsoid.

Cupania hirsuta is closely related to *C. rufescens* and *C. guatemalensis*. It differs from the former in lacking narrow wings on the margins of the capsule

and from the latter in having a subtricornute capsule (i.e., with the lobes of the capsule turned upward) and usually markedly toothed leaflets.

In Panama the species is known to flower only in the dry season. It is known from Costa Rica (Alajuela), Panama, Venezuela, and the Guianas and will doubtlessly be found in Colombia as well. In Panama it is known from tropical moist forest.

BOCAS DEL TORO: Daytonia Farm, Region of Almirante, *Cooper 543b* (BM, F, G, NY, US).

5. **Cupania latifolia** H.B.K., Nov. Gen. Sp. Pl. 5: 126. 1821. TYPE: Colombia, dans l'ile de las Brujas, sur le Magdalena, *Humboldt & Bonpland 1590* (B, not seen, MO, photo).

C. papillosa Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München. 9: 520. 1879. TYPE: Colombia, bassin du Magdalena, Mariguita, *Triana 3468* (G, K, NY).

Trees 4–20 m tall, 5–25 cm d.b.h.; trunk often somewhat twisted, the bark smooth, with fine, granular lenticels which wipe off easily, the inner bark thin, tan, the sap with a faint, pleasant aroma; stems densely lenticellate, the younger parts, including petioles and inflorescence branches, densely brown-tomentose. *Leaves* pinnately 3–11-foliolate (juvenile plants often with some large simple leaves); petioles to 6 cm long, to 15 cm on juvenile leaves; blades oblong-elliptic to obovate, obtuse to truncate and sometimes emarginate at the apex, obtuse to acute and inequilateral at the base, 8–20 cm long, 2–6.5 cm wide, to 35 cm long and 15 cm wide on juvenile leaves, densely short-pubescent to glabrate on the veins above, usually papillate and glabrous to sparsely pubescent and with inconspicuous stalked glands beneath, the margin obscurely crenate to wavy. *Panicles* axillary or subterminal, to ca. 2.5 cm long. *Flowers* white, 2–2.7 mm long; sepals ovate to oblong, tomentose; petals villous, obovate, rounded or emarginate at the apex, the margin fringed, the scale fused to the margins of the petals, deeply divided in the middle; disc thick, bowl shaped, weakly lobed, densely velutinous except on the inner margin; stamens villous below the middle; staminate flowers with the stamens to 3.5 mm long, exserted, the pistillode with 3 minute styles; bisexual flowers with the stamens ca. 1.5 mm long, the ovary ovoid, tomentose, gradually tapered to a stout style, the style and stigma pubescent, together about equalling the ovary, the stigmas 3, ca. 1.5 mm long, divergent. *Capsules* subglobose to 3-lobed, shortly stipitate, to ca. 2.5 cm diam. at maturity, on drying greatly shrinking and becoming more prominently 3-lobed, the valves to ca. 3 mm thick on dried specimens, woody, densely dark brown tomentose outside, woolly inside; seeds ovoid, black, shiny, 1.5 cm long and 1 cm wide, enveloped at the base with an orange yellow aril.

Cupania latifolia is distinguished by its sparsely pubescent leaves which are usually minutely and sparsely papillate and by its large, usually subglobose, densely dark brown tomentose fruits. The species is variable throughout its range, especially in type and amount of pubescence. *Cupania papillosa*, segregated by Radlkofer on the basis of dense papillae and glandular trichomes, is only an extreme form of this species. *Cupania latifolia* is most closely related to *C. cinerea*

and may hybridize with it. *Croat 11981* has pubescence intermediate between the two species.

Cupania latifolia in Panama flowers in June and July with fruits maturing in September and October.

The species ranges from Panama to Colombia, Venezuela, Ecuador, Peru, and Amazonian Brazil. In Panama it is known from tropical moist and tropical wet forests.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 318* (F, GH), *486* (F); *Bangham 373* (F, GH, S, US); *Croat 4887*, *5334*, *5401*, *5848A* (all MO), *6399* (MO, SCZ), *6493* (MO), *6576*, *11076* (both DUKE, F, MO, NY, SCZ), *11471* (MO), *11968* (DUKE, MO, NY, SCZ), *11981*, *14587* (both MO); *Dwyer 1458* (GH, MO, SCZ); *Foster 366*, *399*, *614* (all DUKE), *647* (DUKE, PMA), *1023* (DUKE, MO, PMA), *1477* (DUKE); *Hayden 43* (GH, MO, PMA); *Kenoyer 425* (US); *Salvoza 859* (A, S); *Standley 41072* (US); *Starry 203* (MO), *206* (F). 1 mi beyond Madden Dam Bridge, *Correa & Dressler 350* (MO, PMA). Vic. of Summit Naval Radio Station, *Croat 14098A* (MO). Pipeline Road, 3 mi from Gamboa gate, *Croat 15089* (F, MO, NY). Between Margarita and Gatún, *Croat 15355* (MO). Pipeline Road, 4 miles from Gamboa gate, *Croat 16600* (MO). Madden Dam, Boy Scout Camp Road, *Dwyer & Elias 7481* (GH, MO, US). Coco Solo, *Dwyer & Duke 7907* (GH, MO, US). Madden Dam, Boy Scout Road, *Dwyer 9175* (MO). Gamboa, N of Pipeline Road, *Foster 471* (DUKE). Near Gatún Locks, *Lazor 5488* (SCZ). COLÓN: Steep hill behind Portobelo, *Croat & Porter 15594* (MO). Buena Vista, *Holdridge 6388* (MO, PMA). Río Guanche, *Nee 7136* (CAS, COL, DUKE, F, K, MO, PMA). Río Viejo, 4 km NE of Puerto Pilón, 5 m, *Nee 7176* (C, CAS, GH, MO, PMA, U). PANAMÁ: Vic. of Macambo, *Croat 14901* (F, MO). Cerro Azul, *Croat 17313* (MO). 5–6 mi E of Chepo, *Duke 4040* (GH, MO, US). Vic. of El Llano, *Duke 5522* (MO). Río Terable near Pan-Am. Hwy. and El Llano, *Duke 5658* (MO, SCZ). Headwaters of Río Corso, *Duke 11931* (MO, NY). Río Pasiga, 0–2.5 mi along lumber road to Río Maestro, *Gentry 2339* (MO, PMA). Without exact locality, *Paul 468* (MICH). Around Alejuela, Chagres Valley, 30–60 m, *Pittier 3509* (M, NY, US). 5 mi W of Chepo near Pan-Am. Hwy., *Tyson 6716* (MO).

6. **Cupania livida** (Radlk.) Croat, comb. nov.

Matayba livida Radlk., Repert. Spec. Nov. Regni Veg. 17: 365. 1921. TYPE: Costa Rica, collines de Zent versant atlantique, *Tonduz 14876* (B, destroyed, F, photo).

Trees to 18 m tall and 30 cm d.b.h.; stems densely rufous-tomentose, weakly sulcate when young, terete in age, glabrescent. *Leaves* pinnately 4–9-foliolate, 19–44 cm long; petioles 4–15 cm long; petiolules 3–10 mm long, swollen especially toward the base; petioles, rachises and petiolules densely rufous-tomentose; leaflets oblong-elliptic to oblong-oblanceolate, acuminate to long-acuminate at the apex, acute at the base, sometimes inequilateral and one side to 7 mm shorter than the other, 7–33 cm long, 3.5–10 cm wide, entire or nearly so, the upper surface glabrous or minutely and obscurely puberulent on the midrib, the lower surface densely rufous-tomentose on the major veins, less densely rufous-pubescent over the surface, the major lateral veins 10–13 pairs, ascending sharply near the margin, the secondary lateral veins extending between the primary laterals, the reticulate venation not prominent. *Inflorescences* terminal or from the upper axils, to 20–25 cm long; rachis and pedicels rufous-tomentose. *Flowers* not seen; calyx persistent in fruit, 5-lobed to near the base, the lobes acute, tomentose without, glabrous within. *Fruits* obcordate, 2-lobed, sometimes also with a medial stylar ridge, 1.3–1.7 cm long, about as wide as long, 2-valved, brown to somewhat violet purple, densely short-tomentose without, densely sericeous within,

sessile or short-stipitate; seeds ellipsoid, ca. 1 cm long, black, shiny, glabrous, covered with a thin red aril, at least before maturity.

Flowers for this species are not known, but based on those persisting in fruit, the plant could as easily be *Cupania* as *Matayba*. In every other respect the species more closely approaches *Cupania* than it does *Matayba*, where it was placed by Radlkofer.

Cupania livida is distinguished by its rufous pubescence and 2-lobed fruits. Fruits mature during July and August.

The species is known from Costa Rica and Panama. In Panama it is known only from tropical wet forest in Colón Province.

COLÓN: Río Salud, *Howell 123* (MO). Río Piedras, Portobelo, *Lao & Holdridge 156* (MO). Salud, *Lao & Holdridge 243* (DUKE, MO, PMA).

7. **Cupania rufescens** Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 28: 374. 1862. TYPE: Colombia, Prov. Bogotá, Cuguan et el Morn, *Goudot* (P, not seen).—FIG. 3.

C. schippii Standley, Field Mus. Nat. Hist., Bot. Ser. 12: 411. 1936. TYPE: Belize, *Schipp 1348* (F, GH, NY).
C. fulvida Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 28: 375. 1862. TYPE: Panama, *Hayes 607* (BM, K, W).
C. asperula Standley, Trop. Woods 17: 33. 1929. TYPE: Nicaragua, region of Gragman's Bluff, *Englesing 176* (F, holotype; G, K, NY, isotypes).
C. andina Steyermark, Bol. Soc. Venez. C. Nat. 26: 463. 1966. TYPE: Venezuela, between Bequilla and Mucuchachí, *Steyermark 56301* (F).

Trees to 15 m tall; trunk to 25 cm d.b.h., sulcate at least when young, the bark with shallow, horizontal and vertical fissures, flaking off to expose the reddish inner bark, the wood cream colored, with a sweet odor; younger stems densely ferruginous-hirsute, obscurely 5-ribbed. *Leaves* pinnately 3–7(–9)-foliolate; rachis conspicuously hirsute; leaflets obovate-oblong, mostly rounded at the apex, occasionally obtuse or acute, often inequilateral at the base, the larger leaflets 7–22 (–33) cm long, 3.5–10 cm wide, glabrous above except densely pubescent on the midrib, conspicuously hirsute beneath, especially on the veins, all the veins prominent, the major lateral veins impressed above, the margin entire to usually denticulate (serrate on juvenile plants); simple leaves on juvenile plants to 45 cm long and 15 cm wide. *Panicles* stout and densely floriferous from the upper axils, about equalling the leaves, densely hirsute. *Flowers* white; sepals densely pubescent, 2.8–3.3 mm long, equalling the corolla, regular, not imbricate at anthesis; petals obovate, clawed, pubescent along the margin, the scale fused along the margin at the base; disc orange, prominent, nearly glabrous; stamens with the filaments villous in the lower ¾; staminate flowers opening before the bisexual flowers and mostly deciduous when the bisexual flowers are open, the stamens to 3.5 mm long, exserted, the anthers ca. 1 mm long, attached to the filament at the middle, the thecae divergent in the lower half, the ovary narrowly ovoid, strongly 3-angulate, with a short style and 3 more or less erect stigmas, the stigma and style less than 2 mm long, the ovary and style densely pubescent with stiff, straight trichomes, these usually exceeding the stigmas; bisexual flowers with the

FIGURE 3. *Cupania rufescens* Triana & Planch.—A. Sterile branch (×½). [After *Skutch 3991* (MO), Costa Rica.]—B. Bisexual flower (×4⅘).—C. Petal with attached scales (×9⅗).—D. Stamen (×9⅗).—E. Pistil (7⅕).—F. Fruit (×½). [After *Johnston 642* (MO).]

stamens 2–2.5 mm long, included, the anthers smaller than in the staminate flowers, otherwise similar, the ovary ovoid, ca. 2 mm high, the style about equalling the ovary, the stigmas 3, recurved, exceeding the pubescence. *Capsules* in dense clusters, burnt orange to indian red, sharply 3-sided, 1.5–2 cm broad, nearly as long as broad, densely pubescent without, less so within, dehiscing broadly along the angles; seeds 3, obovoid, ca. 1 cm long, black, shiny, partly enveloped by a yellow to greenish aril.

Cupania rufescens is distinguished by its densely reddish brown hirsute parts and prominently 3-sided capsules that bear a narrow wing around the margin.

It is most easily confused with *C. guatemalensis* but that species has smaller, more obscurely toothed leaves and capsules which show no sign of a winged margin.

The species usually flowers in February and March in Panama with fruits maturing in the late dry season and early rainy season, late April to June. Dehisced fruit valves may hang on the tree all year.

Cupania rufescens ranges from Mexico to Colombia, Venezuela, the Guianas, and Brazil. In Panama it is known from tropical moist, tropical wet, and premontane rain forests. It may be found in mature forest stands.

It is called "candelillo" in Panama.

CANAL ZONE: Barro Colorado Island, *Croat 4815* (MO), *4930* (DUKE, MO, NY, SCZ), *5152* (MO, SCZ), *8244* (MO), *10237* (MO, SCZ), *14036*, *14627*, *14882* (all MO); *Dwyer 1419* (MO); *Foster 2163* (DUKE, GH); *Frost 189* (F); *Oppenheimer 67-5-16* (MO); *Shattuck 664* (MO); *Standley 40990*, *41016* (both US), *Woodworth & Vestal 356* (A). Summit Garden, *Croat 13988* (MO). Vic. of Summit Naval Radio Station, *Croat 14239* (MO, NY). Road K-6 E of Arraiján, *Croat 15037* (MO). Río Grande Station, Panama railroad, *Hayes 607* (BM, K, W). 2 mi W of Balboa, *Luteyn & Foster* 933 (DUKE, F, MO). Around Las Cruces, 20–100 m, *Pittier 2626* (MO, NY). Ancón hospital grounds, 20–80 m, *Pittier 2734* (G, NY). Fort Clayton, *Tyson 1283* (MO, SCZ), *3458* (MO, PMA). DARIÉN: Hill ca. 1 mi NE of Nura, 200 m, *Duke 10079* (MO). Vic. of El Real, Río Tuira, *Stern et al. 749* (G, GH, MO). PANAMÁ: Río Arraijancito, *Cedeño 12* (MO, PMA). Along road to Arraijancito, *Díaz* 33 (MO, PMA). Cermeño, *Dwyer & Robyns 112* (MO). San José Island, *Johnston 571* (BM, GH, S, U), *642*, *1337* (both GH, MO). Chorrera, 100 m, *Lao 71* (DUKE, MO, PMA). Camino de Pacora, *Nash 47* (PMA). VERAGUAS: NW of Santa Fe, 1.5 km from Escuela Agrícola, *Mori & Kallunki 5322* (DUKE, GH, MISSA, MO, PMA, TEX).

8. **Cupania scrobiculata** L. C. Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792. TYPE: Guiana, *Richard* (C, P).

C. reticulata Cambess., Mém. Mus. Hist. Nat. 18: 28. 1829. TYPE: Surinam, *Martin 47* (P).
C. reticulata Spiltgerber, Tijdschr. Natuurl. Gesch. Physiol. 9: 106. 1842. TYPE: Surinam, *Martin* (BR).
C. porosa Miq., Stirp. Surinam. 70. 1850. TYPE: Surinam, *Hostmann 1310* (F, MO, S, U).
C. guianensis Miq., Strip. Surinam. 71. 1850. TYPE: Surinam, *Hostmann 295* (F, GH, K, U, W).
C. frondosa Benth., Hooker's J. Bot. Kew Gard. Misc. 3: 199. 1851. TYPE: Brazil, near Santarem, *Spruce* (GH, K).
C. triloba Triana & Planch., Ann. Sci. Nat. Bot. sér. 4, 18: 376. 1862. LECTOTYPE: Colombia, *Triana 3470* (K).
C. auriculata Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 20. 1930. TYPE: Belize, Stann Creek Railway, 6 miles, *Schipp 267* (F, holotype; G, K, MO, NY, S, Z, isotypes).

Shrubs or small *trees* 3–10 m tall; stems sulcate, puberulent-tomentose to scabridulous when young, glabrate in age. *Leaves* pinnate; petiolules 2–8 mm long; leaflets 6–8, rarely 10–12, elliptic-oblong to ovate, obtuse, subacute or abruptly acuminate at the apex, obliquely acute or cuneate at the base, 5–18 cm long, 2.5–10 cm wide, entire to undulate to sinuate-dentate on the margin, chartaceous, glabrous on both sides except puberulent on the midrib, the reticulate venation prominulous beneath, sometimes also above. *Panicles* axillary or subterminal, 7–30 cm long, equalling or exceeding the foliage; branches densely and minutely cinereous sericeous; bracteoles subulate, 3–5 mm long; pedicels 1–2 mm long, articulate at about the middle. *Flowers* white; sepals ovate or ovate-oblong, to 1.5 mm long, tomentulose outside; petals ca. 1 mm long, equal to the

sepals, broadly ovate, acute, ciliolate, the scale inside the petal broadly obcordate, as long as or longer than the petal, more than twice as wide as the petal, densely villous; stamens 2 mm long, the filaments filiform, pubescent below the middle; disc glabrous below, densely villous above; ovary tomentose; staminate flowers with the stamens 2.5 mm long, the pistil minute; bisexual flowers not seen. *Capsules* stipitate, turbinate, more or less 3-horned, 1–2 cm long, red-tomentose outside, woolly-tomentose inside, the stipe to ca. 3 mm long; seeds oval, ca. 6 mm long.

Cupania scrobiculata may be distinguished by the glabrous lower blade surfaces, the frequent presence of pitlike or weblike axillary domatia in the axils of the veins beneath and by the densely rufous-tomentose, 3-horned fruits.

The species flowers in Panama from December to February, and fruits mature mostly September and October.

It is known from Belize, Panama, Colombia, Venezuela, the Guianas, and Brazil. In Panama it is known from premontane wet and tropical wet forests.

CANAL ZONE: 3 mi NW Gamboa, Navy Pipe Line, *Correa 200* (DUKE, SCZ). Area W of Limón Bay, *Johnston 1559* (MO). Cerro Pelado, 1 km N of Gamboa, 200–220 m, *Nee 6800* (C, DUKE, F, MO, PMA, U, US). Pipeline Road, 4 km NW of Gamboa, 50 m, *Nee 7077* (CAS, GH, D, K, MAD, MO, NY, P, PMA, US, VEN). CHIRIQUÍ: Remedios, 50–100 m, *Pittier 5464* (M, NY, US). COLÓN: Vic. of Camp Piña, *Allen 3678* (D, F, MO, NY, P, U). Santa Rita Ridge, *Gómez-Pompa et al. 3118* (MO). VERAGUAS: 2 km NW of Atalaya, 100 m, *Nee 8199* (F, MO, NY, PMA, US).

9. **Cupania sylvatica** Seem., Bot. Voy. Herald 93. 1853. TYPE: Panama, *Seemann 642* (BM, K, M, S).

9a. **Cupania sylvatica** var. **sylvatica.**

C. seemanni Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 375. 1862. TYPE: Panama, *Seemann* (BM, probably same collection as for *C. sylvatica*).
Talisia svensonii Standley, Contr. Arnold Arbor. 5: 98. 1933. TYPE: Panama, *Woodworth & Vestal 353* (F, MO).

Trees to 8 m tall; trunk to 16 cm d.b.h., often in clumps of 2 or more trunks of various sizes, sometimes with sucker shoots, the bark smooth; younger branches and inflorescences densely rufous-tomentose, otherwise glabrous to inconspicuously puberulent throughout. *Leaves* pinnately 3–7-foliolate, to 45 cm long; petiolule 3–15 mm long, pulvinate; leaflets elliptic, acuminate, sometimes weakly falcate, acute to obtuse at the base, sometimes inequilateral, 4–30 cm long, 1.7–12 cm wide, puberulent on the veins of both surfaces, especially the midrib, the axils of the veins sometimes weakly barbulate beneath; stipules lacking. *Inflorescences* slender, axillary, racemiform thyrses, 1–3 per axil, to 12 cm long; pedicels short, subtended by tiny bracteoles. *Flowers* white, 4–5 mm wide, with a faint sweet aroma, in short clusters of 3, most parts villous; calyx cupular, divided to near the base, the lobes ovate, erect; petals obovate to rhombic, rounded to acute, to 2.7 mm long, the scale nearly as long or longer than the petal, emarginate, fused to the petal along both margins and forming a pocket; ovary rounded, the stigmas 3 in bisexual flowers, absent in staminate flowers. *Capsules* few or many in dense clusters, 3-lobed, broader than long, to 2 cm wide, densely tomentose, bright red

orange to red at maturity, at least at the apex of the capsule, the valves 3, densely silky-pubescent within; seeds 2 or 3, ovoid or subglobose, ca. 1 cm long, 8–10 cm wide, shiny, black, at least the apex exserted from the open capsules, the aril fleshy, white.

Cupania sylvatica is distinguished by its sparsely pubescent leaves and orange to red, densely tomentose fruits. The fruit has an acid but tasty aril.

The species flowers throughout the dry season, late December to May. Fruits mature mostly from March through June.

Collections from higher elevations differ in having more prominently raised reticulate veins and in flowering in the rainy season with fruits developing from September to November. The fruits of this form are, however, indistinguishable from those plants occurring at lower elevations.

Cupania sylvatica is known from Panama and Colombia. In Panama it is known chiefly from tropical moist forest but also from tropical dry and premontane wet forests.

CANAL ZONE: Barro Colorado Island, *Croat 4851* (F, MO, SCZ), *4903*, *5080* (both MO), *5277* (DUKE, MO, SCZ), *5398* (MO), *5543* (DUKE, F, MO, NY, SCZ), *5686* *5706* (both MO, SCZ), *5723* (SCZ), *8387* (MO), 8492, *10164* (both DUKE, MO, NY, SCZ), *10298* (MO), *13481* (DUKE, F, MO, NY, PMA), *13483* (MO), *14003* (DUKE, F, MO, NY, PMA), *14086*, *14613* (both MO), *14988* (DUKE, F, GH, MO, NY), *15063* (MO); *Foster 532* (PMA), *767* (DUKE, F, PMA), *782* (DUKE, F, MICH, PMA); *Kenoyer 670* (US); *Oppenheimer 66-5-20-1110* (MO); *Standley 31422* (US); *Svenson 425* (F); *Woodworth & Vestal 353* (F, MO), *459* (A, F, MO); *Zetek 3465* (F, MO). Radar Station Road, *Blum et al. 2345* (MO, SCZ). Madden Forest Road, 2 mi marker, *Croat 8955* (MO, SCZ). Pipeline Road, 3–4 mi N of Gamboa, *Gentry 3350* (DUKE, MO). Pipeline Road, near gate, *Gentry 4898* (F, MO, U). Near Río Frijoles, *Gentry 5823* (MO). Between Pipeline Road and Frijoles, *Gentry 7461* (MO, PMA, RSA, TEX, VEN). Empire, *Hayes 115* (BM, M). Between Chagres Batteries and Fort San Lorenzo, *Maxon & Valentine 7030* (C, US). Across from Summit Gardens on Summit Naval Base, *Mori & Kallunki 6482* (MO, PMA). Vic. of Summit Gardens, 100 m, *Nee 10204* (MO, PMA). Summit Gardens, *Nee 11324* (DUKE, F, MO, PMA, NY, US). Culebra, 50–150 m, *Pittier 3432* (US). Around Gamboa, *Pittier 4804* (US). Forêts de Cruces et Gorgona, *Seemann 642* (BM, K, M, S). Vic. of Río Cocoli, *Stern et al. 29*, *31A* (both GH, MO). DARIÉN: Río Pirre, *Duke & Bristan 8312* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1475* (MO, NY). Around Pinogana, *Pittier 6533*, *6536* (US). PANAMÁ: Cerro Campana, 100 m, *Gentry 5766* (MO). Taboga Island, *Pittier 3628* (M, US). W slope of Cerro Campana, *Tyson & Godfrey 2362* (SCZ). WITHOUT EXACT LOCALITY: *Boudier s.n.* (P).

9b. **Cupania sylvatica** var. **fosteri** Croat.[7] TYPE: Panama, *Foster 1343* (DUKE-219087, holotype; DUKE, F, GH, MICH, MO, PMA, isotypes).

Trees to 5 m tall, sometimes growing in clumps; stems terete, tomentose when young, glabrate. *Leaves* pinnately 4–6-foliolate, 10–20 cm long; petioles 10–25 mm long, tomentose to glabrate in age; petiolules 1–5 mm long; leaflets elliptic, oblong-elliptic to narrowly ovate, acute to bluntly acute at the apex, acute to obtuse at the base, sometimes weakly inequilateral, 4–15 cm long, 2–5.5 cm wide, glabrous above, glabrous beneath except for the axillary domatia and sometimes the sparsely puberulent major veins near the axils. *Inflorescences* slender, axil-

[2] *Cupania sylvatica* Seem. var. *fosteri* Croat, var. nov. Differt a varietate typica foliolis glaberis praeter aream prope axillas nervorum lateralium infra foliolium et retibus minoribus prominentibus.

lary, spikelike or paniculate, to ca. 10 cm long; pedicels bracteate, appressed-pubescent. *Flowers* white, to 3.5 mm wide; calyx cupular, divided to near the base, appressed grayish pubescent without, less densely so within, the lobes ovate, erect; petals obcordate, ca. 1.5 mm long, villous, the scale ovate, rounded to acute at the apex, free nearly to the base, villous, ca. 1 mm long; disc lobed, densely villous; stamens 3–4 mm long, villous; staminate flowers with the pistil densely pubescent; bisexual flowers with the stamens less than 1 mm long, the pistil ovoid, densely tomentose, the style short. *Capsules* 3-lobed, obcordate, broader than long, ca. 1.5 cm wide, orange, sparsely puberulent to strigose, the surface visible and shiny, the inner surface densely silky pubescent.

Variety *fosteri* is distinguished from the typical variety by the nearly glabrous leaves, presence of tufted vein axils (sometimes also with pitted domatia as well), and sparsely appressed-pubescent capsules. It also differs from the typical lowland form of var. *sylvatica* by flowering in the late rainy season rather than in the dry season. Flowering collections are known only from November.

In Panama, *Cupania sylvatica* var. *fosteri* is known from tropical moist forest. It is named in honor of Robin Foster, its first collector.

CANAL ZONE: Barro Colorado Island, *Foster 1343* (DUKE, F, GH, MICH, MO, PMA). PANAMÁ: Road to Cerro Campana, Su Lin, ca. 800 m, *Kennedy 1532* (F, K, MO, PMA, US, VEN). VERAGUAS: 2 km NW of Atalaya, 100 m, *Nee 8199* (MO).

5. DIPTERODENDRON

Dipterodendron Radlk., Smithsonian Misc. Collect. 61(24): 5. 1914. TYPE: *D. elegans* Radlk.

Large *trees*; stems terete, conspicuously lenticellate, glabrate. *Leaves* bipinnate, exstipulate, large; leaflets small, to 20 on each pinnule, pinnately veined, serrate on the margin. *Thyrses* in the axils of the apical leaves, subequal. *Flowers* small; sepals 5, pubescent; petals absent; stamens 6–8, long exserted. *Capsules* 2- or 3-lobed, 2- or 3-loculate, pubescent to glabrous outside, tomentose inside; seed arillate.

Three species have been described for this genus, two from Costa Rican material and a third from Venezuela. They do not differ greatly. One of the Costa Rican species is known from Panama.

1. **Dipterodendron costaricense** Radlk., Smithsonian Misc. Collect. 61(24): 5. 1914. TYPE: Costa Rica, Alejuela Prov., La Balsa de Río Grande, *Pittier 3645* (US).—FIG. 4.

Large *trees*, 15–40 m tall, to more than 1 m d.b.h.; sap malodorous; young stems terete, slightly sulcate, glabrous or pilose at the apex, the lenticels conspicuous. *Leaves* bipinnate, 30–70 cm long; pinnae alternate to subopposite, deciduous, 7–14 cm long; rachis and rachilla puberulent; leaflets more or less oblong, rounded to acuminate at the apex, inequilaterally acute at the base, the lower edge more acute, 10–40 mm long, 6–12 mm wide, glabrous, shiny, the reticulate veins prominulous, the margin crenate-serrate throughout most of its length. *Thyrses* 8–18 cm long, borne in the axils of the apical leaves; pedicels

FIGURE 4. *Dipterodendron costaricense* Radlk.—A. Sterile branch (×6/10).—B. Fruit (×1⅕). [After *Duke* 5818 (MO).]

1–1.5 mm long. *Flowers* greenish; perianth more or less rotate, to 2 mm wide, lobed to about the middle, densely pubescent, the lobes rounded-acute at the apex; petals absent; stamens to ca. 3 mm long, the filaments nearly glabrous or only sparsely pubescent, narrowly tapered to the apex, the anthers broadly oblong, ca. 1 mm long; disc thick, densely tomentose, not noticeably lobed. *Capsules* ovoid to globose, 2.5–3 cm diam., reddish, the pericarp 2 mm thick, glabrate to granular-tomentose outside, tomentose inside; seeds 1.5–1.8 cm long, thick, black, shiny, enveloped at the base by a thin, white aril.

This species is distinguished from other Sapindaceae in Panama in being a tree with bipinnate leaves bearing many small leaflets. Common names in Darién include "harino" and "jarino."

The species flowers in April and May, mid to late dry season, and fruits mature mostly in the early rainy season (June) but have also been seen in December.

Dipterodendron costaricense is known from Costa Rica and Panama. In Panama it is known from tropical moist forest. Standley (1928) reported the species to occur on the Pacific watershed. *Dipterodendron elegans*, which differs from *D. costaricense* mostly in being conspicuously appressed-pubescent, also occurs in Costa Rica. The third species in the genus, *D. venezuelense* Steyermark, appears to be intermediate between *D. elegans* and *D. costaricense*. More collections may show all of these to constitute a single species.

CHIRIQUÍ: Without exact locality, *Cooper & Slater 280* (F, GH, NY). DARIÉN: Without exact locality, *Duke 8220* (MO). Near Refugio, 15–20 mi N of Santa Fe, ca. 30 m, *Duke 10266* (DUKE, MO). PANAMÁ: Vic. of El Llano, *Duke 5818* (MO).

6. DODONAEA

Dodonaea Miller, Gard. Dict., abr. ed. 4. 1754. TYPE: *D. viscosa* (L.) Jacq.

Empleurosma Bartl. in Lehm., Pl. Preiss. 2: 228. 1847. TYPE: *E. virgata* Bartl. = *Dodonaea pinifolia* Miq.

Shrubs or small *trees*. *Leaves* alternate, simple or pinnate; stipules absent. *Thyrses* terminal or lateral, solitary, racemose, corymbose or paniculate. *Flowers* unisexual or polygamo-dioecious; sepals 2–5, imbricate or valvate; petals absent; disc obsolete in the staminate flowers, small in the pistillate flowers; stamens 5–8, the filaments short, the anthers linear-oblong, obtusely tetragonous; style 3- to 6-parted, the ovules 2 in each cell. *Fruits* membranous or coriaceous capsules, 2- to 6-angled, the cells 1- or 2-seeded, the angles acute, obtuse or broadly winged; seeds obovoid, subglobose or lenticular, lacking an aril, the testa crustaceous or coriaceous; embryo circinate.

Radlkofer (1933–1934) lists 54 species, all but 2 of which are found in Australia. One species is found in tropical America.

1. **Dodonaea viscosa**[8] (L.) Jacq., Enum. Pl. Carib. 19. 1760.—FIG. 5.

Ptelea viscosa L., Sp. Pl. 118. 1753. TYPE: not seen.

Dioecious *shrubs* or *trees* 2–5 m tall; wood brown, close grained, hard; stems reddish, angled, glabrous, minutely fissured and lenticellate. *Leaves* oblong-lanceolate to linear-lanceolate, simple, sessile or short-petiolate, acute to rounded at the apex, attenuate at the base, 5–12 cm long, 1.5–5 cm wide, viscid and glabrous, the margin entire. *Thyrses* axillary or terminal, shorter than the leaves, racemiform or corymbiform. *Flowers* pale yellowish; sepals usually 4, ca. 3 mm long; petals absent. *Capsules* suborbicular, winged, obcordate, cordate at the base, 2.2 cm long, 2.5 cm wide, 3-winged, 3-locular; seeds lenticular, black.

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[8] For more synonymy see Radlkofer (1933–1934). Only the names cited here relate directly to Panamanian material.

FIGURE 5. *Dodonaea viscosa* L.—A. Flowering branch (×6/10).—B. Bisexual flower (×6). [After *H. S. Gentry 2015* (MO), Mexico.]—C. Fruit (×12⅕). [After *Stern et al. 1940* (MO).]

Duke (1968) reports that an infusion of the leaves is used for fevers. Common names are "hopbush" (English), "hayuelo" (Spanish).

Dodonaea viscosa can be distinguished by its long, narrow, viscid, simple leaves.

In Panama the phenology of the species is not well known. It has been collected in flower and fruit throughout the year elsewhere in Central America. Most collections have been made in the dry season from December to April.

The species is widely distributed in the tropics of the world. It is more common elsewhere in Central and South America, especially in the dry regions of the Andes. In Panama it is known only from the western highlands and from near the Caribbean coast. Elsewhere in Central America it is reportedly common on arid serpentine soils.

BOCAS DEL TORO: Vic. of Almirante, Changuinola Canal, *Blume 1390* (MO, SCZ). Changuinola Valley, Bar Mouth, *Dunlap 480* (F, US). CHIRIQUÍ: Boquete, 5500 ft, *Davidson 1295* (US). Llanos S of Boquete, *Stern et al. 1940* (MICH, MO). Volcancitos, *Terry 1259* (A, F, MO). PANAMÁ: 2 km NE of Jorco, *Wilbur et al. 15998* (DUKE). VERAGUAS: Mouth of Río Concepción, *Lewis et al. 2848* (SCZ).

7. FILICIUM

Filicium Thwaites, Enum. Pl. Zeyl. 408. 1864, new name for *Pteridophyllum* Thwaites.

Pteridophyllum Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 65, *tab. 1.* 1854, non Siebold & Zucc., 1843 (Papaveraceae). TYPE: *P. decipiens* (Wight & Arn.) Thwaites = *F. decipiens* (Wight & Arn.) Thwaites.

Jurighas O. Kuntze, Rev. Gen. Pl. 1: 144. 1891. TYPE: *J. decipiens* (Wight & Arn.) Kuntze = *F. decipiens* (Wight & Arn.) Thwaites.

Small and medium-sized, polygamous *trees*. *Leaves* pinnately compound, leaflets 2–10 pairs, subopposite or alternate, linear-oblong or obovate, entire, oblique at the base, sessile, bearing sunken lepidote scales on the upper surface; rachis winged. *Inflorescences* terminal or axillary, paniculate. *Flowers* regular, small; sepals 5, persisting; petals 5, small; disc plate shaped, densely pubescent on the upper surface; stamens 5, inserted in depressions of the disc, glabrous, the anthers introrse, basifixed, rudimentary in female flowers. *Fruit* ovoid or ellipsoid, drupaceous, 1–2-loculate, the endocarp membranous; seeds 1–2; embryo curved.

The genus has three species in tropical Africa and Asia. A single species, *F. decipiens* (Wight & Arn.) Thwaites is cultivated occasionally in Panama.

1. **Filicium decipiens** (Wight & Arn.) Thwaites in Thwaites & Hook., Enum. Pl. Zeyl. 408. 1864.

Rhus decipiens Wight & Arn., Prodr. Fl. Penin. Ind. Orient. 172. 1834. TYPE: not seen.
Pteridophyllum decipiens (Wight & Arn.) Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6: 65. 1854.
Jurighas decipiens (Wight & Arn.) Kuntze, Rev. Gen. Pl. 144. 1891.

Small or medium-sized, polygamous *trees*; younger branches weakly sulcate with lepidote scales. *Leaves* pinnately compound, glabrous, 25–30 cm long, the

rachis prominently winged, the wing broader toward the apex; leaflets subopposite or alternate, in 2–4 pairs, oblong-linear or oblong, 4–10 cm long, 1–2 cm wide, acute and minutely emarginate at the apex, inequilaterally acute at the base, sessile, entire, viscidulous on both surfaces, the upper surface shiny with many sunken lepidote scales, the reticulate veins obscure, the major lateral veins numerous, the lower surface with prominulous reticulate veins. *Panicles* terminal and from the uppermost leaf axils, 13–20 cm long; pedicels glabrate to sparsely strigose, to ca. 4 mm long. *Flowers* with the sepals narrowly ovate, to 5 mm long, narrowly rounded at the apex, glabrate on the outer surface, villous along the margins and on the inner surface; petals ovate, 1.5 mm long, glabrous on the surfaces, ciliolate; disc plate shaped, woolly on the upper surface; stamens exserted, the filaments flattened, glabrous; staminate flowers with the stamens ca. 2.5 mm long, the anthers ovoid, ca. 0.5 mm long, the pistil ovoid, minute, glabrous; pistillate flowers not seen. *Fruit* drupaceous, ovoid, 1–1.5 cm long, smooth, dark purple.

The species is rarely cultivated on streets in Panama City. It can be recognized by a combination of its compound leaves, winged rachis, drupaceous fruits, and arborescent habit.

The species is native to Africa and Asia.

PANAMÁ: Panama City, *Holdridge 6381* (PMA).

8. MATAYBA

Matayba Aubl., Hist. Pl. Guiane 1: 331, *tab. 128*. 1775. TYPE: *M. guianensis* Aubl.

Ernstingia Scop., Introd. 322. 1777. TYPE: Based on *Matayba* Aubl.
Ephielis Schreb., Gen. Pl. 1: 253. 1789. TYPE: Based on *Matayba* Aubl.
Ratonia DC., Prodr. 1: 618. 1824. TYPE: *R. domingensis* DC. = *Matayba domingensis* (DC.) Radlk.

Polygamous *shrubs* or *trees*; stems terete, sulcate, lenticellate, the young branches usually pubescent. *Leaves* alternate to subopposite, even-pinnate, long-petiolate, exstipulate; leaflets mostly entire, usually thick. *Inflorescences* axillary or terminal, paniculate or racemiform. *Flowers* regular, white, small; calyx cupulate, 5-lobed to near the base, the lobes deltoid; petals 5, rarely rudimentary, usually contracted into a long slender claw, bearing a scalelike appendage within, the scales villous; disc regular, fleshy and annular; stamens 8, the filaments subfiliform, often pubescent; ovary subglobose or obovoid, 3-lobed, with 2 locules, densely pubescent, the style terminal, the stigma 2- or 3-dentate; ovules 1 in each cell, inserted at the middle of the axis. *Capsules* ellipsoid-subglobose or obovoid, 3-lobed or slightly winged, sessile or stipitate; seeds ellipsoid, arillate, with crustaceous testa.

About 45 species are found in tropical America. Four species are known from Panama.

a. Leaflets serrate; axils of the veins beneath foveolate (with a distinct pit) .. 4. *M. scrobiculata*
aa. Leaflets entire; axils of the veins beneath barbulate or glabrous, not foveolate.

b. Leaflets 2 (1 pair) ..... 3. *M. kennedyi*
bb. Leaflets usually 4 or more (2 or 4 pairs).
c. Lower side of leaflets with the axils of the veins barbulate; petiolules and leaf rachises glabrous or inconspicuously short-pubescent; disc of the flower tomentose; capsules glabrate outside ..... 1. *M. glaberrima*
cc. Lower side of leaflets with the axils of the veins glabrous; petiolules and leaf rachises with coarse, long, brownish trichomes; disc of the flower glabrate; capsules densely brown-tomentose outside ..... 2. *M. ingaefolia*

1. **Matayba glaberrima** Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9: 535. 1879. TYPE: Mexico, *Haenke* (B, destroyed, MO, photo).—FIG. 6.

Shrubs or small *trees* 4–11 m tall; stems terete, glabrous. *Leaves* pinnate, 8–25 cm long; leaflets 2–6, obovate-oblong to elliptic, obtuse to acute or bluntly acuminate at the apex, acute to attenuate at the base, 4.5–17(–20) cm long, 1.3–6 (8) cm wide, entire, revolute, coriaceous, glabrous, often drying brownish at least beneath, the pits in the axils of the veins beneath barbulate. *Panicles* terminal or subterminal, 10–15 cm long, shorter than the leaves; pedicels appressed-pubescent. *Flowers* white, ca. 2.5 mm long; calyx lobed more than half way to the base, the lobes ovate to deltoid, less than 1 mm long, appressed-pubescent with a dense tuft of trichomes at the apex; petals deltoid or ovate, 0.5–1 mm long, ½–⅔ as long as the scales, the scales ca. 0.5–1.5 mm long, divided to the base or nearly so, each obovate to rounded, glabrate to sparsely pubescent on the outer surface, densely pubescent inside; disc weakly lobed, glabrate on the marginal surface, densely short-villous on the upper surface; staminate flowers with the stamens ca. 1.5 mm long, the filaments densely villous in the lower half, the anthers ca. 0.5 mm long, as broad as long, the pollen tacky, pale yellow, the ovary ovoid, densely pubescent, minute; pistillate flowers with stamens ca. 1.3 mm long, the pistil ca. 3 mm long, the ovary and style equally long, the ovary 3-sided, appressed-pubescent, the style weakly appressed-pubescent. *Capsules* reddish to purple violet, bluntly 3-lobed, ca. 1.5 cm long and 1 cm wide, abruptly long-stipitate, glabrous outside except on stipe, glabrous inside, the septae long-sericeous; stipe 3–4 mm long; seeds bluish, obovoid, shiny, white-arillate, ca. 1 cm long.

It is distinguished by its stiff, obovate leaf blades with tufted, pitlike domatia in the vein axils of the lower leaf surfaces. While *Matayba scrobiculata* and *Cupania scrobiculata* also have pitlike domatia, the fovea are glabrous.

Erlanson 81 was distributed by the Gray Herbarium as the type of *Talisia porteriana* Johnston, but the name was never published.

Matayba glaberrima flowers in April and May in Panama. Fruits normally mature between May and September.

The species ranges from Mexico to Panama. In Panama it is ecologically variable occurring in tropical dry forest, premontane moist forest, tropical moist forest and premontane wet forest.

The species is called "baralazo" in Panama.

CANAL ZONE: Victoria Fill near Miraflores Locks, *Allen 1757* (F, GH, MO, NY, US). Ancón Hill, *Bartlett & Lasser 16310* (MICH). Albrook Forest, *Blum 2234* (DUKE). Summit

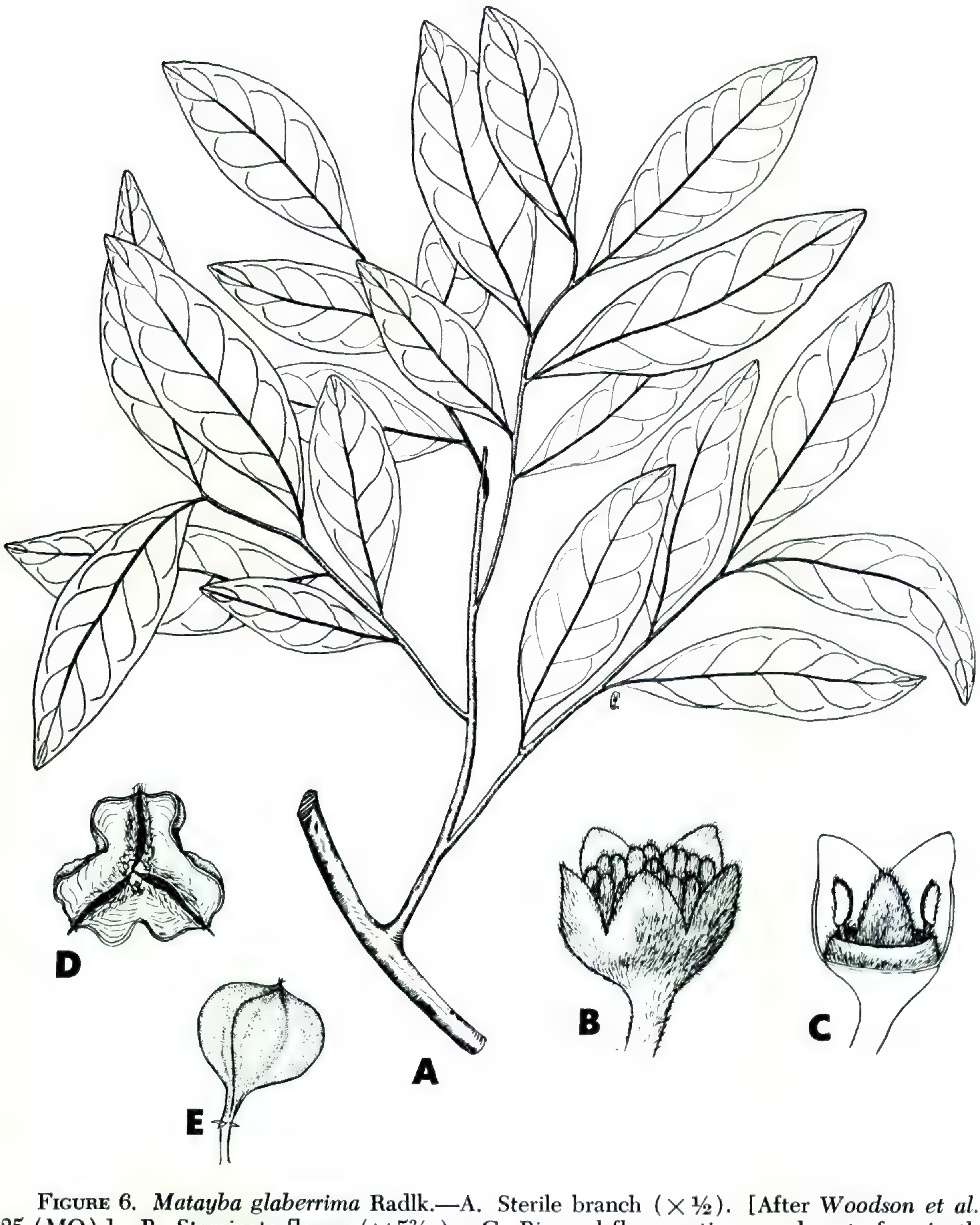

FIGURE 6. *Matayba glaberrima* Radlk.—A. Sterile branch (×½). [After *Woodson et al.* 725 (MO).]—B. Staminate flower (×5 3/10).—C. Bisexual flower, stigma and part of perianth and androecium removed (×5 3/10). [After *Allen 1757* (MO).]—D. Open capsule, top view (× 1 1/10). [After *Dwyer 1151* (MO).]—E. Unopened fruit (×1 1/10). [After *Croat 13824* (MO).]

Garden, *Croat 13824* (MO). ¾ mi S of Summit Golf Club, *Croat 14665* (DUKE, MO, NY, SCZ). Road CZ toward Chiva-Chiva, *Croat 14909* (DUKE, F, MO, NY, SCZ). Vic. of Fort Kobbe beach, *Duke 4204* (MO). Albrook USATTC test site, *Dwyer & Robyns 63* (MO). Mandingo Road, *Hayden 55* (MO). Albrook, *Holdridge 6416* (MO, PMA). Summit Gardens, *Mori & Kallunki 4541* (MO). Howard Air Force Base, *Oliver & MacBryde 1879* (GH, MO, SCZ). Vic. of Río Cocolí, Road K-9, *Stern et al. 33* (G, GH, MO, US). Fort Clayton, *Tyson*

& *Blum 3919* (MO). 12 mi S Colón on Río Providencia, *Tyson & Blum 3943* (DUKE). Chiva-Chiva Trail near Miraflores Lake, *Tyson & Blum 4010* (DUKE, MO). COCLÉ: El Valle, *Allen 3703* (F, G, MO). El Valle de Antón, *Lao 285* (MO, PMA). LOS SANTOS: 1–2 mi W of Candelana, *Duke 12434* (MO). Las Tablas, *Dwyer 1151* (MO, NY). PANAMÁ: Cermeño, *Dwyer & Robyns 137* (MO). San José Island, *Erlanson 81* (GH, MO, NY, US); *Johnston 225* (GH), *709* (GH, MO, US), *731*, *792* (both GH). Just N of Lidice, *Kirkbride & Duke 1686* (MO, NY). E of Bella Vista, *Maxon & Valentine 6964* (US). Alrededores de Chame, *Moron 20* (DUKE, MO, PMA). Savannas N of Panama City, *Paul 468* (US). Punta Paitilla, *Piper 5423*, *5436* (both US). Taboga Island, *Pittier 3575* (M, US). Chepo, 60 m, *Pittier 4563* (US). Sabana de San Juan Corso, near Chepo, *Pittier 4671* (US). Río Mar, sea level, *Spellman et al. 527* (MO). Punta Paitilla, *Standley 26264* (US). Near big swamp E of Río Tocumen, *Standley 26681* (US). Taboga Island, *Standley 27037* (US). Vic. San Juan Race Track near Panama City, *Standley 27774* (US). Tumba Muerta Road near Panama City, *Standley 29721*, *29819* (both US). Between Las Sabanas and Matías Hernández, *Standley 31878* (US). East of Pacora, 25 m, *Woodson et al. 725* (A, F, MO). VERAGUAS: 4 mi from Pan-Am. Hwy. toward Ponuga, *Dwyer & Kirkbride 7430* (DUKE, MO). Ca. 5 mi W of Santiago, *Tyson 6669* (PMA). WITHOUT EXACT LOCALITY: *Seemann s.n.* (BM).

2. **Matayba ingaefolia** Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 224. 1929. TYPE: Panama, *Cooper 597* (F, US).

Small *trees* to ca. 8 m tall; stems terete, rufous-tomentose when young, becoming glabrate. *Leaves* pinnate; petiolule and rachis usually with long, coarse, reddish-brown persistent trichomes; leaflets 2–4 pairs, lanceolate or narrowly lanceolate-oblong, long-acuminate at the apex, obtuse to acute at the base, 3–15 cm long, 1.3–5 cm wide, entire, membranous, glabrous on both sides, sometimes pubescent on the prominently raised midrib above and along the major veins beneath. *Panicles* axillary, racemiform, 3–10 cm long; pedicels 2–3 mm long, articulate in the lower ⅓, sparsely pubescent below the articulation. *Flowers* ca. 4 mm long; calyx bowl shaped, 2.5–3 mm diam., divided almost to the base, the lobes oblong-ovate, acute at the apex, ca. 1 mm long, viscid-puberulous outside, glabrate inside; petals white, narrowly oblong, acute at the apex, gradually tapered to the base, 2 mm long, the scales nearly as long as the petals, fused to the lower ⅓ of the petal, deeply bifid to the point of insertion, each part narrowly spatulate, ciliate, villous; disc plate shaped, the margin thin, undulate, glabrous or sparsely pubescent, one edge turned up forming 2 semicircular lobes; stamens villous in the lower half; staminate flowers with stamens 3–3.5 mm long, the anthers small, broader than long, the pistil minute, densely tomentose; bisexual flowers not known. Immature *capsules* subglobose, to 12 mm long, 2-lobed, sessile, bilocular, densely reddish-brown tomentose outside, densely long sericeous inside.

Matayba ingaefolia is most easily confused with *M. glaberrima* but can be distinguished by its densely brown-tomentose fruits and by the long, coarse, brownish trichomes on the petioles and leaf rachises.

The species flowers in February and April. In Panama it is known from wetter regions of middle elevations on the Caribbean slope in western Panama. It may also occur in Costa Rica.

BOCAS DEL TORO: Region of Almirante, Buena Vista Camp on Chiriquí Trail, 3000 ft, *Cooper 597* (F, US). Between Buena Vista coffee finca and Cerro Pilón, *Kirkbride & Duke 707* (MO). VERAGUAS: NW of Santa Fe, 4.2 km from Escuela Agrícola Altos de Piedra, *Mori & Kallunki 4828* (COL, DUKE, F, MO, NY, PMA, RSA).

3. **Matayba kennedyi** Croat.[9] TYPE: Panama, *Kennedy 2523* (MO-2158953, holotype).

Trees ca. 4 m tall; stems minutely and inconspicuously grandular-tomentose when young, soon glabrous, terete, the periderm grayish. *Leaves* 2-foliolate; petioles terete, ca. 3 cm long, glabrous to sparsely and inconspicuously puberulent, often glandular; leaflets ovate to narrowly ovate, bluntly acute to acuminate at the apex, obtuse to rounded at the base, 6–15 cm long, 3–7.5 cm wide, entire, glabrous except sometimes sparsely puberulent and glandular on the midrib beneath, drying dark brown, the major lateral veins mostly 5 or 6 pairs, turning sharply upward just before merging with the margin; stipules inconspicuous. *Inflorescences* axillary, branched or unbranched, to ca. 10 cm long, sparsely rufous-tomentose; pedicels puberulent, to 4.5 mm long in fruit, articulate about midway. *Flowers* not seen. *Capsules* reddish, ellipsoid to obovoid, 1.5–2 cm long, (2–)3-lobed, sometimes irregularly so, appressed-puberulent outside, glabrous inside except for the dense rufous-villous pubescence near the base of the capsule; seeds ellipsoid, black, shiny, glabrous, ca. 7 mm long.

Matayba kennedyi is distinguished by its 2-foliolate, glabrous leaves. It is known only from the type collected with mature fruits in February in tropical wet forest in Panama.

PANAMÁ: 19 km above Pan-Am. Hwy. on road from El Llano to Cartí Tupile, *Kennedy 2523* (MO).

4. **Matayba scrobiculata** (H.B.K.) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 9: 536. 1879.

Cupania scrobiculata H.B.K., Nov. Gen. Sp. Pl. 5: 127. 1821, non L.C. Rich., 1792. TYPE: Colombia, near Turbaco (not seen).

Trees 5–15 m tall; stems subterete, occasionally sulcate, puberulent when young, the epidermis grayish, thin, shiny. *Leaves* pinnate, 10–30 cm long; leaflets obovate-oblong to obovate, retuse, truncate or rounded at the apex, attenuate to acute at the base, 3–8 cm long, 1.5–5.5 cm wide, membranous, glabrous on both sides, scrobiculate-foveolate in the vein axils beneath, the margins serrate-dentate to obtusely serrate. *Panicles* axillary near the apex of the stem, subequal to the leaves, to 25 cm long, pedicels mostly less than 1 mm long, to 2.5 mm long in in fruit, articulated in the middle. *Flowers* small, yellow-green; calyx scarcely 1 mm long, deeply lobed, the lobes acute, tomentulose outside; petals suborbicular, ca. 1 mm long, abruptly contracted into a claw, the margin villous; disc glabrous, lobed; stamens 2.5–3 mm long, the filaments glabrous. *Capsules* obcordate-pyriform, abruptly stipitate, glabrate outside, glandular inside, 1–1.5 cm long, becoming reddish at maturity, the stipe to ca. 3 mm long; seeds obovoid, arillate, 1 cm long.

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[9] *Matayba kennedyi* Croat, sp. nov. Arbor ad 4 m alta. Folia bifoliolata, praeter petiolum costamque puberulum glabra. Inflorescentia axillaris, circa 10 cm longa, rufa-tomentosa. Flores ignoti. Capsula elliptica ad obovata, 1.5–2 cm longa, (bi-)trilobata, rufa.

The species is distinguished by its mostly oblong-oblanceolate, truncate or retuse leaf blades with pits in the lower vein axils. It is apparently not close to any other species in Panama.

Matayba scrobiculata flowers in Panama in the early dry season, from January to March. Fruits mature in the early rainy season, probably later than June.

Matayba scrobiculata is known from Mexico to Panama, Colombia, Venezuela and Bolivia. In the Canal Zone the species occurs along the edges of roads in disturbed forest. It is known from tropical moist forest, premontane moist forest, and tropical dry forest.

The species is called "baralazo" in Panama.

CANAL ZONE: Near Miraflores Locks, *Allen 1708* (F, MO, NY, US). Vic. Miraflores Dam, *Correa 1184* (MO, PMA). Ancón Hill, *Croat 4513* (MO, SCZ). Ancón, near Tivoli, *Croat 8880* (MO). Without locality, *Hayes 113* (BM). Balboa, *Holdridge 6412* (MO, PMA). Summit Gardens, *Johansen 71* (US), *76* (MO). Ancón Hill, *Pittier 6504* (M, US). Balboa, *Standley 27145* (MO, US). Fort Clayton, *Tyson & Blum 2904* (DUKE, MO). Pedro Miguel, *Tyson & Lazor 6158* (SCZ). CHIRIQUÍ: Forests around Remedios, 0–30 m, *Pittier 3384* (US). DARIÉN: Patino, *Pittier 5700* (M, NY, US). LOS SANTOS: Las Tablas, *Dwyer 1151* (MO). Vic. of Tonosí, Ocho Paso, a small tributary of Río Tonosí, *Stern et al. 33645* (MICH, US). PANAMÁ: Isla Chepillo, *Duke 10321* (MO). Vic. Panama City, *Macbride 2606* (F, G, US). Saboga Island, *Duke 10364* (MO); *Miller 1956* (MO, US). Taboguilla Island, *Miller 2002* (MO, US). Pacora, *Paul 269* (US). Taboga Island, *Standley 27983* (US). Juan Díaz, *Standley 30460* (US). Nuevo San Francisco, *Standley 30730* (US). WITHOUT EXACT LOCALITY: *Maxon & Valentine s.n.* (US).

9. MELICOCCUS

Melicoccus P. Browne, Civ. Nat. Hist. Jam. 210. 1756. TYPE: *M. bijugatus* Jacq.

Polygamous, dioecious, or rarely monoecious, small to medium-sized *trees*. *Leaves* sparse, exstipulate, petiolate, paripinnate with 1 or 2 pairs of leaflets; leaflets opposite, subsessile, entire, pinnately veined. *Inflorescences* terminal; pedicels filiform, nonarticulate; bracteoles minute, subulate. *Flowers* regular; calyx 4-lobed, the lobes imbricate, the two outer lobes smaller; petals 4, lacking scales; disc orbicular, crenate to 4-lobed; stamens 8, inserted within the disc around the pistil or pistillode. *Fruits* indehiscent, 2- or rarely 3-locular, subglobose drupes; seeds ellipsoid, nonarillate.

The genus has two species in South America. At least one is widely cultivated in Central America.

1. **Melicoccus bijugatus** Jacq., Enum. Pl. Carib. 19. 1760. TYPE: Jamaica (not seen).

Mellicocca bijuga L., Sp. Pl., ed. 2. 495. 1762. TYPE: America meridional (not seen).

Polygamous, deciduous, slow-growing *trees*, 6–20 m tall; trunk to 60 cm d.b.h., slightly angled and fluted, the bark gray, smooth, the inner bark orange brown, granular; stems grayish, glabrous. *Leaves* paripinnate, to 26 cm long; petioles 1.5–7 cm long, sometimes winged near the apex; rachis winged or not; leaflets 2–4, elliptic to ovate-elliptic, acute to acuminate, acute and inequilateral at the base, nearly sessile, 7–14 cm long, 2.5–6 cm wide. *Inflorescences* terminal, the branches

slender; racemes many flowered, simple or paniculate; pedicels slender, to ca. 3.5 mm long. *Flowers* white, 6–8 mm diam.; calyx deeply 4- or 5-lobed; petals obovate, to 3 mm long, ciliolate; disc broadly spreading, glabrous, weakly lobed; stamens 8–10; staminate flowers with the stamens to 3.5 mm long, the pistil lacking; bisexual flowers with the stamens to ca. 1.5 mm long, the ovary shorter than the petals, ovate, abruptly narrowed at the apex beneath the capitate, 2-lobed stigma. *Drupes* green to pale yellow, globose, 2–3 cm diam., the pericarp ca. 2 mm thick, smooth, the mesocarp yellowish, translucent, sweet and juicy; seeds globose, 1.5–2 cm diam.

Melicoccus bijugatus flowers in Panama in the dry season (January to April). Fruits mature in the rainy season.

The species is native to northern South America (Colombia to the Guianas). It is introduced and widely cultivated elsewhere in the tropics.

Common names for this species are numerous and include: "genip," "ginep" (Virgin Islands, U.S., Panama); "mamon" (Panama, Spain); "mamoncillo" (Colombia, U.S., Spain); "quenepa" (Dominican Republic); "escanjote" (Nicaragua); "mamon de cartegena" (Costa Rica); "spanish lime" (U.S.); "chenet" (Trinidad); "quenep" (Haiti); "guenette," "guenettier," "kenepier" (French territories); "kenepa," "kinnup-tree," "knippen" (Dutch territories).

CANAL ZONE: Summit Gardens, *Mori & Kallunki 4539* (MO). PANAMÁ: Cerca de los silos del IFE, *Almillategui 18* (DUKE, MO, PMA). Panama City, *Lao 469* (MO).

10. PAULLINIA

Paullinia L., Sp. Pl. 365. 1753; Gen. Pl., ed. 5. 170. 1754. TYPE: *P. pinnata* L.

Enourea Aubl., Hist. Pl. Guiane 1: 587. 1775. TYPE: *E. capreolata* Aubl. = *Paullinia capreolata* (Aubl.) Radlk.

Semarillaria Ruiz & Pavón, Fl. Peruv. Chil. Prodr., ed. 1. 54. 1794. LECTOTYPE: *S. subrotunda* Ruiz & Pavón = *Paullinia subrotunda* (Ruiz & Pavón) Pers.

Castanella Spruce ex Benth. & Hook., Gen. Pl. 1: 394. 1862. TYPE: *C. granatensis* Planch. & Linden ex Triana & Planch. = *Paullinia granatensis* (Planch. & Linden) Radlk.

Polygamous, tendrilled, scandent *shrubs* or *lianas*; wood simple or composite, usually with a central bundle surrounded by 3 peripheral bundles; milky sap common in stems; tendrils axillary or peduncular, forked, often bracteate at the fork, the arms coiled like a watchspring. *Leaves* alternate, 1-foliate, 3-, 5-, or 7-foliolate, biternate, ternate-pinnate or bipinnate; petiole and rachis often winged; leaflets membranous to coriaceous, often pellucid-punctate or -lineate, often with a network of semipellucid lactiferous canals (orange colored when observed by transmitted light), the margin usually variously toothed, the teeth often glandular; stipules often conspicuous, usually persistent. *Inflorescences* axillary, subterminal or at leafless nodes, usually solitary, sometimes fascicled, then at leafless nodes, basically thyrses but sometimes modified into cincinni and borne on a raceme, panicle or cyme, the cincinni subtended by bracts, the flowers with bracteoles. *Flowers* small, slightly zygomorphic; sepals 5 or 4 by fusion of the 2 lower sepals, imbricate, persistent, the 2 outside sepals smaller, often persisting in fruit; petals 4, with a complex, crested scale within, the scale consisting

of an ellipsoid to rounded, petaloid, ciliate, basal part with a thickened, usually orange, variously shaped crest at the apex and a semicircular or triangular, usually densely pubescent, deflexed appendage positioned just beneath the crest on the inner surface, the anterior petal scales better developed than lateral petal scales, often coherent along their common inner margin by the entanglement of trichomes, the lateral petal scales with the crests reduced or absent, the basal part usually oblong, folded inward with the margins in proximity; disc annular, produced into 2 or 4 glands, usually only the anterior glands developed, these positioned beneath the anterior petals and usually protruding into the space formed by the lateral upfolded margins of the anterior petal scales and by the deflexed appendages; stamens unequal, the anthers dehiscing laterally, the filaments often weakly basally united in staminate flowers; ovary 3-locular, sessile or short-stipitate, each cell 1-ovular, the style subulate or filiform, the stigma 3-parted, the ovules solitary, affixed below the middle of the cell. *Fruits* capsular, 1–3-celled, each cell 1-seeded, dehiscent into 3 valves, obovate or subglobular, sessile or stipitate, the valves septicidal, wingless, winged at the apex or winged for the total length of each cell, rarely spinose; seeds short, usually arillate with a crustaceous testa, sometimes completely enveloped in mesocarp and apparently non-arillate; embryo usually curved.

About 194 species are known from tropical America. One species, *P. pinnata*, also occurs in Africa.

The genus is difficult to distinguish in flower from *Serjania*, especially the trifoliolate and biternate-leaved species, since both genera share these leaf types. Careful observation of the ovary and immature fruits will distinguish the fruit type and thus the genus. *Serjania* has the ovary noticeably swollen and broader at the apex with thinner wings. *Paullinia* ovaries, even when the fruit will become markedly winged, do not appear distinctly winged in flower and they are generally elliptic or rounded in outline rather than oblong or obovate as in *Serjania*.

a. Leaves pinnately 3-foliolate (3 leaflets borne on a petiole) or biternate (3 sets of 3 leaflets each borne on a petiolule).
  b. Leaves 3-foliolate.
    c. Petioles not winged; stems terete ..... 37. *P. turbacensis*
    cc. Petioles winged, at least narrowly so; stems terete or 3-sulcate.
      d. Stems terete usually with simple wood; inflorescences simple, unbranched, axillary in existing leaves ..... 11. *P. cururu*
      dd. Stems deeply 3-sulcate with composite wood (3 small bundles surrounding a larger one); inflorescences compound, branched, densely glomerulate, borne at old leafless stems ..... 17. *P. fasciculata*
  bb. Leaves biternate (3 sets of 3 leaflets).
    e. Rachis not winged or rarely narrowly winged, the wing less than 3 mm wide ..... 5. *P. brenesii*
    ee. Rachises broadly winged, the wing 3 mm wide or more.
      f. Stems, petioles, and rachises conspicuously hispid; flowers and fruits borne on leafless stems ..... 8. *P. correae*
      ff. Stems, petioles, and rachises not at all hispid; flowers and fruits borne in existing leaf axils.
        g. Capsules wingless, long-stipitate; (difficult to separate vegetatively from *P. fuscescens*), leaves usually lobate-crenate, rounded at the apex; flowers widely spaced on the rachis ..... 9. *P. costaricensis*

gg. Capsules 3-winged, short-stipitate; leaves crenate, commonly acute at the apex.
h. Leaves glabrous or nearly so beneath except for the barbulate vein axils; flowers clearly pedicellate, less than 3.5 mm long, nearly glabrous; fruits nearly glabrous ..... 20a. *P. fuscescens* var. *glabrata*
hh. Leaves densely pubescent beneath; flowers sessile or nearly so, 3.5–4.5 mm long, densely and conspicuously pubescent on the sepals; fruit densely and conspicuously pubescent ..... 20b. *P. fuscescens* var. *fuscescens*

aa. Leaves pinnately 5-foliolate, 7-foliolate, bipinnate or ternate-pinnate.
i. Leaves merely pinnate, either 5-foliolate or 7-foliolate, leaflets not arranged in 3's at the base of the blade.
j. Leaves 7-foliolate.
k. Stems, petioles, and rachises conspicuously hispid; rachises winged ..... 26. *P. panamensis*
kk. Stems, petioles, and rachises not at all hispid; rachises terete ..... 25. *P. morii*
jj. Leaves 5-foliolate.
l. Petioles terete or at least not winged.
m. Leaf rachis winged.
n. Stems prominently 4–6-ribbed; inflorescences associated with the leaves.
o. Inflorescences terminal; stipules ovate to suborbicular, fimbriate-dentate marginally, less than 1.5 cm long; capsules thin, not winged ..... 35. *P. stipularis*
oo. Inflorescences axillary or on tendrils; stipules lanceolate, entire, more than 1.5 cm long; capsules thick, prominently winged ..... 3. *P. baileyi*
nn. Stems terete; inflorescences borne at leafless nodes.
p. Inflorescences of few-flowered fascicles less than 1 cm long; fruits almost round in outline, as broad as or broader than long ..... 8. *P. correae*
pp. Inflorescence with slender, many-flowered branches more than 4 cm long; fruits obovoid in outline, longer than broad ..... 13. *P. dodgei*

mm. Leaf rachis not winged.
q. Young stems, petioles, rachis and midrib of the blades densely reddish brown hirtellous-tomentose or shortly tomentose.
r. Pubescence of stems and petioles conspicuously erect, easily visible to the naked eye; lower midrib, veins and surface hirtellous to pilose with erect pubescence; leaflets commonly ovate.
s. Stipules suborbicular, deeply lacerate, more than 10 mm wide; leaflets commonly more than 15 cm long; plants common ..... 30. *P. rugosa*
ss. Stipules lanceolate, entire, less than 5 mm wide; leaflets less than 15 cm long; plants rare ..... 12. *P. dasystachya*
rr. Pubescence of stems and petioles not conspicuously erect, often appressed, very short and not easily visible to the naked eye; lower midrib and veins minutely strigose, the surface mostly glabrous; leaflets mostly oblong-elliptic or obovate-elliptic ..... 16. *P. faginea*
qq. Stems, petioles, rachis and midrib of the variously pubescent or glabrate not densely reddish brown hirtellous-tomentose nor shortly tomentose.
t. Outer sepals densely tomentose or strigose throughout; fruits not winged; (sepals unknown in *P. dukei*).
u. Fruits acuminate-mammillate at the apex, with 3 ridges indicating lines of dehiscence, prominently stipitate, the stipe 3–6 mm long; seeds black, shiny, enveloped to about midway by a white aril; inner surface of fruit densely woolly-tomentose and the surface not at all visible ..... 10. *P. costata*
uu. Fruits rounded at the apex, sometimes with a small, slender

style base persisting, lacking ridges or 6-sulcate, sessile or with the stipe less than 3 mm long; seeds not shiny or black, enveloped in a fleshy mesoderm, not arillate at the base; inner surface of the fruit either glabrous or sparsely and loosely pubescent and the surface easily visible.

v. Leaflets glabrous; fruits subglobose, 6-sulcate with a small persistent style base, shortly stipitate, reportedly dull yellow ..... 27. *P. pilonensis*

vv. Leaflets puberulent on the midrib; fruits obovoid, smooth, lacking a persistent style base, sessile, reportedly "brown maroon" (probably violet purple) ..... 14. *P. dukei*

tt. Outer sepals sparsely appressed or spreading-pubescent to glabrous, not densely strigose or tomentose; fruits winged or not.

w. Inflorescences borne at leafless nodes, branched from near the base (thus almost appearing fasciculate), the branches long and slender, more than 6 cm long; flowers with scale crests simple, long and slender; fruits not winged ..... 36. *P. tenuifolia*

ww. Inflorescences usually borne at leafy nodes, the thyrses either solitary and unbranched or, if rarely fasciculate, then the branches short, less than 3 cm long; flowers with scale crests short, obovate, emarginate to rounded at the apex; fruits winged or not.

x. Fruits not winged ..... 14. *P. dukei*

xx. Fruits winged (fruits of *P. allenii* are assumed to be winged because of its close affinity with *P. subnuda* and *P. pterocarpa*).

y. Stipules oblong, blunt at the apex, conspicuously villous marginally, densely pubescent on the inner surface, soon deciduous; inflorescences to 12 cm long; flowers to ca. 5–6 mm long ..... 2. *P. allenii*

yy. Stipules lanceolate-linear, almost glabrous, persistent; inflorescences apparently always much shorter than 12 cm; flowers to ca. 4 mm long .. 29. *P. pterocarpa*

ll. Petioles winged (sometimes narrowly so in *P. eliasii*).

z. Inflorescences glomerulate or fasciculate, often at leafless nodes, the thyrses not solitary except perhaps in fruit after other parts have fallen; stems prominently 3-ribbed.

A. Inflorescences densely glomerulate, the thyrses less than 2 cm long, branched; wood composite, consisting of a central bundle surrounded by 3 smaller bundles.

B. Inflorescence branches and pedicels conspicuously erect-pubescent; crest of anterior scales cordate-bifid; leaf rachis with wings to ca. 1 cm wide ..... 1. *P. alata*

BB. Inflorescence branches and pedicels glabrate to inconspicuously appressed-puberulent; crest of anterior scales obovate; leaf rachis with wings ca. 5 mm wide ..... 17. *P. fasciculata*

AA. Inflorescence sparsely fasciculate, the thyrses to 6 cm or more long, unbranched; wood simple, deeply divided but not of separate bundles (sometimes splitting apart on drying and appearing to be 3 separate bundles) ..... 15. *P. eliasii*

zz. Inflorescences spicate, solitary in the leaf axils; stems variously ribbed or terete.

C. Stems terete; fruits usually nearly globose, mammillate, prominently stipitate, the stipe slender, 3–7 mm long ..... 18. *P. fibrigera*

CC. Stems prominently 3–6-ribbed; fruits ellipsoid to obovoid or clavate, or if globose, not at all stipitate.

D. Bracteoles of the inflorescence narrowly triangular to ovate-triangular; stipules frequently more than 1.5 cm long.

E. Axils of the lateral veins not barbulate on the lower sur-

face; stipules more than 4 mm wide near the base; fruits more than 1.5 cm diam. ---- 4. *P. bracteosa*

EE. Axils of the lateral veins barbulate on the lower surface; stipules less than 4 mm wide; fruits less than 1.5 cm wide ---- 32a. *P. sessiliflora* var. *angustirachis*

DD. Bracteoles of the inflorescence lanceolate or lanceolate-linear; stipules usually less than 1.5 cm long or soon deciduous.

F. Fruits globose, sessile, glabrous; leaves often entire, glabrous except for the barbulate vein axils; wood simple ---- 6. *P. bristanii*

FF. Fruits clavate to obovoid, somewhat to greatly stipitate, pubescent or glabrous; leaves usually toothed; wood composite, the central core surrounded by 3 small peripheral cores.

G. Sepals less than 3 mm long, finely and sparsely appressed-pubescent in flower and fruit, glabrate and thin when persisting in fruit; fruits long-stipitate, the stipe often more than 4 mm long; leaves somewhat thickened; plants common ---- 28. *P. pinnata*

GG. Sepals to 5 mm long, coarsely and densely appressed-pubescent in fruit (flowers not known), thick when persisting in fruit; fruits short-stipitate, the stipe often less than 4 mm long; leaves thin; plants rare ---- 33. *P. sternii*

ii Leaves bipinnate or ternate-pinnate, the leaflets in sets of 3 at the base of the blade.

H. Inflorescences not densely fasciculate, not short and finely branched, usually more than 2 cm long.

I. Rachis not winged, terete; bracteoles conspicuous, ovate-triangular, more than 5 mm long; stems terete; wood simple ---- 22. *P. grandifolia*

II. Rachises winged; bracteoles inconspicuous, lanceolate, less than 3 mm long; stems weakly to strongly sulcate; wood simple or composite.

J. Wood composite with 1 central and 3 peripheral bundles; leaflets moderately thick, drying brownish on the lower surface, densely brown-glandular over the surface; crest of scale probably obovate-emarginate, much shorter than the petals ---- 34. *P. stipitata*

JJ. Wood simple; leaflets thin, drying green, eglandular; crest of scale linear, about as long as the petals ---- 7. *P. buricana*

HH. Inflorescences densely fasciculate and/or short and finely branched, less than 2 cm long.

K. Stems terete or only weakly ribbed, not prominently 3-sided or 3-ribbed; wood simple.

L. Lateral veins numerous, arising at about 90° from the midrib; reticulate venation prominulous on both surfaces ---- 23. *P. kallunkii*

LL. Lateral veins few, at least those near the base ascending at ca. 45° from the midrib; reticulate venation prominulous or not on both surfaces.

M. Stems and petioles conspicuously yellowish-hispid ---- 8. *P. correae*

MM. Stems and petioles not at all hispid, mostly glabrous.

N. Leaflets with vein axils barbulate beneath with dense tufts of trichomes; flowers usually at leafless nodes distant from the leaves; fruits more than 2.5 cm wide ---- 31. *P. serjaniaefolia*

NN. Leaflets with vein axils not barbulate beneath; flowers often in close association with the leaves; fruits less than 1.5 cm wide ---- 21. *P. glomerulosa*

KK. Stems prominently 3–5-ribbed; wood often composite.

O. Inflorescences not fasciculate and not appearing so, usually a single, short, widely branched thyrse, the pedicels much

shorter than the floral rachis; pubescence of petioles conspicuous, erect, more than 1 mm long ..... 19. *P. funicularis*

OO. Inflorescences densely fasiculate or so short as to appear so, usually of numerous shortly branched thyrses, the pedicels as long as or longer than the floral rachis; pubescence of petioles lacking or not conspicuous, erect and usually less than 0.5 mm long.

P. Fruits less than 1.5 cm wide, densely pubescent, prominently long-stipitate; flowers and fruits usually borne with or near leafy parts of the stem ..... 24. *P. mallophylla*

PP. Fruits more than 2.5 cm wide, glabrous or nearly so, sessile; flowers and fruits borne well below the leaves ..... 31. *P. serjaniaefolia*

1. **Paullinia alata** (Ruiz & Pavon) G. Don, Gen. Syst. 1: 660. 1831.

Semarillaria alata Ruiz & Pavon, Fl. Peruv. Chil. 4: *tab. 340.* 1802. TYPE: Peru, Chicoplaya, *Ruiz & Pavon* (B, not seen).

Paullinia rhizantha Poepp. & Endlich., Nov. Gen. Sp. Pl. 3: 36, *pt. 243.* 1844. TYPE: Peru, Dept. of Loreto, Yurimaguas, *Poeppig 2239* (F).

Paullinia metensis Cuatr., Revista Acad. Colomb. Ci. Exact. 4: 347. 1941. TYPE: Colombia, Los Llanos, Río Meta, La Perra, near Cano de Aricaporo, 120 m, *Cuatrecasas 4308* (US).

Lianas; stems 3-angled, villous when young, glabrate and shiny in age; wood composite with a single central core surrounded by 3 peripheral bundles, the peripheral bundles sometimes divided into 2 bundles each. *Leaves* pinnately 5-foliolate, 18–40 cm long; petiole broadly winged, usually 5–10 mm wide; petiolules ca. 4 mm long, densely pubescent; leaflets elliptic to obovate, acuminate at the apex, cuneate to acute at the base, often shortly rounded on to the petiole, 5–21 cm long, 3–12.5 cm wide, membranous, glabrous except for the midrib above and the barbulate vein axils beneath, the margins crenate to serrate-dentate from beyond the middle; stipules narrowly triangular, less than 3 mm long, glabrous, soon deciduous. *Thyrses* glomerulate-fasciculate in the axils of the leaves of older stems or on tendrils, the rachis sparsely villous, to 2 cm long, usually short; pedicels 3–5.5 mm long, sparsely puberulous, usually articulate ca. 1 mm below the flower. *Flowers* white, greenish white or with a yellow calyx and white petals; sepals ovate, ca. 3 mm long, glabrous; petals obovate-oblong, 3–4 mm long, glabrous, the scales of both anterior and lateral petals ca. 3 mm long, broad at the base, narrow at the middle, ciliate on the margins, the crest large, equalling the basal part, cordate-bifid, glabrous, the deflexed appendage of the anterior petals triangular, marginally ciliate; disc glands about as broad as long, glabrous, subtending the anterior petals only; stamens to 3 mm long, the filaments glabrous or villous. *Fruits* 3-celled, obovate, long stipitate, wingless, with a tumid projection at the apex of each carpel, 1.5–2 cm long, weakly striate, glabrous, red; seeds 3, ellipsoid, laterally compressed, ca. 1 cm long, the aril extending to midway on each side.

The species may be confused with *Paullinia pinnata, P. sessiliflora* var. *angustirachis* and *P. bracteosa* but is distinguished from the first two species by its glomerulate inflorescence and from the last by its much smaller fruit and barbulate vein axils on the lower leaf surface.

Paullinia alata flowers in Panama from June through October, and fruits mature from September through January or sometimes as late as March.

The species ranges from Costa Rica south to the Amazon Basin in Peru and Bolivia. In Panama it is known from tropical moist and premontane wet forests.

Juvenile plants (*Croat & Porter 15518, 15499*) may have the older stems terete.

BOCAS DEL TORO: Water Valley, *von Wedel 853* (GH, MO, US). CHIRIQUÍ: Quebrada Quanabanito beyond La Repressa W of Puerto Armuelles, *Croat 22047* (MO). San Bartolo Arriba, W of Puerto Armuelles, 125 m, *Croat 26698A* (MO). Tolé, vic. of Santa Ana Well, ca. 1000 ft, *Dwyer & Kirkbride 7461* (MO, SCZ). Vic. of San Félix, 0–120 m, *Pittier 5139* (M, US). DARIÉN: Río Pirre, *Croat & Porter 15499* (MO), *15517* (MO, SCZ), *15518* (MO). Chepigana District, *Davidson et al. 1394* (F). Without exact locality, *Duke 5019* (MO). Vic. of Caná, 1750 ft, *Stern et al. 474* (G, GH, MO, US). PANAMÁ: Sabanas near Chepo, 30 m, *Allen 25* (F). Río Bayano above confluence with Río Chepo, *Duke 4003* (GH, MO, US). Between Cañazas and Sabalo, 100 m, *Duke 14452* (MO). Sabanas near Chepo, 30 m, *Hunter & Allen 25* (F, GH, K, MO, NY, P, S, US). Mamoni River above Chepo, 20–25 m, *Pittier 4736* (M, NY, US). Just S of La Capitana, *Tyson 6761* (MO).

2. **Paullinia allenii** Standley, Ann. Missouri Bot. Gard. 27: 315. 1940. TYPE: Panama, *Allen 1657* (MO-1191195, holotype; F, GH, US, isotypes).

Lianas or small *trees* with scandent branches; stems 4- or 5-angled, glabrous; tendrils present on new growth; wood simple. *Leaves* pinnately 5-foliolate; petiole and rachis wingless; leaflets narrowly oblong-lanceolate to ovate or elliptic-lanceolate, sharply acuminate, obtuse or acute to rounded at the base, 9–15 cm long, 2.5–4(–7) cm wide, glabrous, barbulate in the vein axils beneath, entire or serrate to serrate-dentate above the middle, the teeth glandular; stipules deciduous, oblong, bluntly acute at the apex, 8–12 mm long, glabrous on the outer surface, densely appressed-puberulent within, conspicuously villous along the margin. *Inflorescences* axillary, solitary, the thyrses in a slender raceme, to ca. 12 cm long. *Flowers* white, to 5 mm long, ca. 6.5 mm wide; sepals oblong-lanceolate, ca. 4 mm long, glabrous; petals obovate-elliptic, 5–6 mm long, glabrous, the scale of the anterior petals ca. 4 mm long, pilose on the margin, the deflexed appendage deltoid, densely white-bearded marginally, mostly in the lower ⅓, the crest bilobed or truncate, as long as the deflexed appendage, the lateral scales with the crest slender, rounded at the apex; disc glands higher than wide, concave outside, appressed-pubescent in the lower half; bisexual flowers with the stamens to 4 mm long, the filaments flattened, basally united, sparsely arachnoid-pubescent; ovary 3-sided, glabrous, together with the style ca. 1 mm long. *Fruits* not known.

The species is most similar to *Paullinia pterocarpa* and additional collections may show the two species to be synonymous. *Paullinia allenii* apparently differs from *P. pterocarpa* in having larger flowers, longer inflorescences, and deciduous, oblong, blunt stipules which are densely pubescent within. *Paullinia allenii* is also similar to *P. subnuda* Radlk. from Brazil and the Guianas. Although the fruit is unknown, it is believed to be similar to that of *P. pterocarpa* and *P. subnuda*, i.e., narrowly 3-winged, elliptic-obovate.

Paullinia allenii is known only from Panama and was collected in flower during February in tropical wet forest.

COCLÉ: N rim of El Valle, 600–1000 m, *Allen 1657* (F, GH, MO, US).

3. **Paullinia baileyi** Standley, Contr. Arnold Arbor. 5: 95, *pl. 14.* 1933. TYPE: Panama, *Bailey & Bailey* 59 (F).

Lianas; stems 6-ribbed with milky sap; wood simple; stems, petioles and midribs of leaflets conspicuously pilose to hispid with yellowish brown trichomes 1–6 mm long. *Leaves* pinnately 5-foliolate, 13–40(–60) cm long; petioles 1–12(–19) cm long, without wings; rachis winged, 4–11(–15) mm wide, often broadest in the upper half; leaflets elliptic or elliptic-oblong to oblanceolate or obovate, gradually acuminate at the apex, acute to attenuate at the base, the lower pair often rounded or subcordate, 2.5–22(–30) cm long, 1.5–11(–15) cm wide, remotely dentate; stipules paired, lanceolate, to 3 cm long, ciliate. *Inflorescences* short, densely glomerulate thyrses in the leaf axils or borne on tendrils. *Flowers* white, 5–5.5 mm long; sepals oblong, glabrous; petals ca. 4 mm long, oblong to obovate, acute, the scales ca. 3.5 mm long, the margins villous, the crests yellow, oblong, about as long as the basal part, thin, rounded to emarginate at the apex, the deflexed appendages only ca. half as long as the crest, truncate, villous, short-villous along the margin; disc glands erect, flattened, slightly longer than broad; staminate flowers with the stamens ca. 3 mm long, the filaments glabrate, fused into a basal tube, the ovary 3-angled, ca. 1 mm long, glabrous; bisexual flowers with 3 styles held above the staminal tube. *Capsules* reddish, suborbicular, 1–1.5 cm long, 3-celled, prominently 3-winged, glabrous; seeds 1 or 2, oblong-obovate, solitary, dark, shiny, the lower ⅓ covered with a white aril.

The species is similar to *Paullinia correae* but is distinguished by stems prominently 6-ribbed and densely covered with trichomes 3–6 mm long and by fruits less than 1.5 cm wide. Flowers and fruits are most often associated with leafy parts of the plant. *Paullinia correae*, on the other hand, has terete stems with trichomes less than 2 mm long. Stems soon become glabrate and fruits are usually greater than 2 cm wide. The flowers and fruits of *P. correae* are usually on a woody stem well below and not associated with the leafy parts of the plant.

P. baileyi flowers in the dry season from March to May. Fruits mature during the late rainy season and early dry season, sometimes apparently persisting until flowering time the following year.

The species is known only from Panama in wetter parts of tropical moist forest and in premontane rain forest. It may also occur in tropical wet forest since it has been collected several times in the vicinity of Cerro Jefe and at least part of that region is tropical wet forest.

BOCAS DEL TORO: Vic. of Chiriquí Lagoon, *von Wedel 2292* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 59* (F); *Croat 4000A* (F, MO, SCZ), *5683* (MO), *8723* (MO, SCZ), *10318*, *10875*, *11276*, *14067* (all MO); *Foster 773*, *2304* (both DUKE); *Kenoyer 623* (US); *Montgomery 89* (MO); *Shattuck 25* (F, MO); *Shattuck 152* (A, MO, US); *Standley 31300*, *40925* (both US), *Wetmore & Woodworth 857* (A, F). Between Locks and Fort Sherman, *Croat 15365* (MO). Pipeline Road, *Smith & Smith 3301* (F, MO). COLÓN: Santa Rita Ridge Road, *Mori & Kallunki 2074* (MO). PANAMÁ: 2.4 mi beyond Cerro Jefe on road to Altos de Pacora, 800–1000 m, *Croat 22652* (MO). Campo Tres, beyond Cerro Jefe, ca. 700 m, *Croat 27074* (MO). Piriá-Cañazas Trail near Piriá, 100 m, *Duke 14319* (MO). Cerro Jefe, 3100 ft, *Dwyer & Gentry 9439* (MO, SCZ); *Gentry 4885B* (F, MO, U). NE slope of Cerro Jefe, *Tyson et al. 3247* (MO, SCZ).

4. **Paullinia bracteosa** Radlk., Bull. Herb. Boissier 2: 321. 1905. TYPE: Costa Rica, buisson du Tuis, 650 m, *Tonduz 16416* (F, NY, US).

P. naiguatensis Steyermark, Bol. Soc. Venez. Ci. Nat. 26: 457. 1966. TYPE: Venezuela, Distrito Federal, Cerro Naiguata, 900–1100 m, *Steyermark 91874* (US).

Lianas; young stems 5-sulcate, the older stems with 3 broad corky wings; sap milky; wood composite, usually with 3 inconspicuous peripheral bundles; stem, petiole and rachis with sparse long pubescence. *Leaves* pinnately 5-foliolate; petioles to 22 cm long, winged; rachis winged, 6–24 mm wide; leaflets elliptic, oblong-elliptic or obovate, usually abruptly acuminate at the apex, obtuse to attenuate at the base, 8–30 cm long, 4–12 wide, weakly bullate at least in age, glabrous above except for the hirsute midrib and the weakly pubescent principal veins, glabrate to hispidulous throughout below, the midrib often both hispid and puberulent, crenate above the middle, the teeth glandular; blades, rachis and petiole with margins ciliate; stipules paired, lanceolate, 2–4 cm long, to 1.5 cm wide, minutely pubescent and ciliate. *Inflorescences* cylindrical, axillary, stout, ca. 2.5 cm wide, 10–20 cm long, densely rufous-tomentose, bracteolate. *Flowers* white; sepals to 5.3 mm long, suborbicular, concave, tomentulose, ciliolate; petals equalling or exceeding the sepals, glabrous except for appressed pubescence outside medially in the lower ⅔ of the petal, the scales ⅔–¾ as long as the petal and nearly enclosed within the concavity of the petal, the scale margins and margins of the deflexed appendage prominently bearded with stiff, white trichomes, the crest ca. 1 mm long, entire, orange; disc glands of the anterior petals whitish, erect, flattened, broader than high, densely pubescent at the base; stamens 7 or 8, the filaments densely villous throughout, to 3 mm long, held closely together around the pistil, the anthers ovate-elliptic, the connective dark, the thecae whitish; staminate flowers with ovary bearded at the base, the 3 styles short and reduced, held well below the anthers; bisexual flowers with styles 3-branched to below the middle, to 2.3 mm long, held well above the anthers, the unbranched part pubescent. *Capsules* pyriform, 3–5 cm long, rounded to subcordate and apiculate at the apex, tapered to the base, terete to broadly 3-sided, 3-celled, the valves thick, to ca. 3 mm diam., striate, densely puberulent to glabrous without, glabrous within; seed 1 (rarely 2), to 2 cm long, enveloped throughout by a red mesoderm, the aril apparently lacking.

Paullinia bracteosa may be confused with several other species possessing 5-foliolate leaves with winged rachises and winged petioles. However, it is distinguished by the large, nonarillate fruits and the weakly bullate older leaves. It is most easily confused with *P. sessiliflora* var. *angustirachis* which differs in having smaller fruits and shinier and usually narrower leaflets which are glabrous except for the barbulate axils of the lower surface.

Radlkofer (1933–1934) reported *P. eriantha* Benth. for Panama based on *Hayes 334* from the Canal Zone but that collection is *P. bracteosa*. *Paullinia eriantha* is a South American species which differs in having a more pubescent, ellipsoid fruit.

In Panama, *P. bracteosa* flowers from the early dry season to the early rainy season, December to August, and fruits mature mainly from February to August.

The species ranges from Costa Rica (Caribbean slope and Osa Peninsula) south to Venezuela and to the southern parts of the Amazon Basin from the Rio Madeira in Brazil to Peru and Bolivia. In Panama it is restricted to tropical moist forest.

BOCAS DEL TORO: Above RR stop at Milla 7.5, *Croat & Porter 16302* (MO). Vic. of Chiriquí Lagoon, *von Wedel 1250, 1336* (both GH, MO, US). CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 283* (F); *Bangham 446* (A), *542* (A, F, GH); *Croat 4530* (MO), *4814* (DUKE, F, MO, NY, SCZ), *4954, 5291, 5363* (all MO, SCZ), *5818, 7177* (all MO, NY, SCZ), *10394* (F, MO, SCZ), *10395* (SCZ), *11655, 14005, 14588, 16589A* (all MO); *Foster 1022* (DUKE, MO, PMA); *Kenoyer 421* (US); *Montgomery 62, 79, 155* (all MO); *Pittier 4011* (C, GH, M, NY, US); *Salvosa 542* (A); *Shattuck 620* (F, MO, US); *Standley 31281* (US); *Starry 99, 313* (both F, MO); *Wetmore & Abbe 206* (A, F, GH, MO), *222* (A, F, MO); *Wetmore & Woodworth 38* (F), *869* (A); *Wilson 64* (F); *Woodworth & Vestal 570* (A, MO); *Zetek 3466* (F, MO). Pipeline Road, 4 mi from Gamboa gate, *Croat 16690* (MO). Pipeline Road, *Gentry 1446B* (MO). Cerro Galera, *Gentry 6644* (MO). Pipeline Road, Limbo Hunt Club, *Kennedy & Kennedy 3055* (MO). CHIRIQUÍ: Puerto Armuelles, *Davidson 1140* (F). DARIÉN: Río Tuquesa, ca. 2 air km from continental divide, *Croat 27230* (MO). El Real Quebrada, *Duke 327* (MO). Slopes of Cerro Chucula, drainage of Río Pavarando, *Gentry 4250* (MO). Vic. of El Real, *Stern et al. 779* (G, GH, MO, US). LOS SANTOS: Vic. of Tonosí, Guanaco, *Stern et al. 33665* (US). PANAMÁ: Río Peta, 1–3 mi above confluence with Río Maestra, *Duke 4733* (GH, MO). Río Pasiga to above waterfall on 2nd main fork, *Gentry 2307* (MO). 4 mi E of Cañitas, *Gentry 4973* (MO). Along Río Chilibre, *Piper 5680* (US). SAN BLAS: Mainland opposite Playón Chico, 0–200 m, *Gentry 6383* (MO). WITHOUT EXACT LOCALITY: *Hayes 334* (K).

5. **Paullinia brenesii** Croat.[10] TYPE: Panama, *Croat 26906* (MO-2205418, holotype; CAS, COL, CR, DUKE, F, GH, K, MEXU, NY, P, PMA, RSA, TEX, U, US, VEN, isotypes).

Lianas; stems terete, densely brown-tomentose when young, glabrate and somewhat purplish in age, the persistent pubescence in narrow, straight bands alternating with reddish brown strips of periderm; wood simple. *Leaves* biternate; petioles 1.5–4.5 cm long, terete to margined or rarely narrowly winged and usually broadest in the upper half; petiole and rachis pubescent; leaflets ovate to ovate-elliptic or obovate, obtuse to bluntly acute or rarely acuminate at the apex, attenuate at the base, 2–8(–10) cm long, 1–4.5 cm wide, conspicuously crenate to crenate-lobate, the surfaces viscidulous, usually conspicuously pubescent on both surfaces with usually erect, curved trichomes, the upper midrib sharply raised, more densely pubescent than the surface, the axils of the lower lateral veins barbulate; juvenile leaves more distinctly lobate, to 18 cm long and 7 cm wide. *Thyrses* in terminal panicles to 10–20 cm long, the branches, pedicels, bracteoles, and calyces densely grayish- or brown-tomentose; bracteoles narrowly deltoid, to ca. 2.5 mm long; pedicels 3–4 mm long, articulated about midway. *Flowers* white, ca. 5 mm long; sepals ovate to elliptic, densely appressed-pubescent within; petals obovate, ca. 4 mm long, the scales 3 mm long, ciliate, the crest semicircular to obovate, orange, glabrous, the deflexed appendage longer than

[10] *Paullinia brenesii* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex. Folia biternata; petiolus nuda vel raro anguste alata; foliola 2–8(–10) cm longa, 1–4.5 cm lata. Inflorescentia terminalis. Fructus ruber, stipite ad circa 3 mm longo, late obovatus, circa 12 mm longus, plerumque manifeste alatus.

the crest, densely villous along its margin; disc glands thick, semicircular, finely pubescent inside; stamens villous, flattened; staminate flower with the stamens to 4 mm long, the pistil ca. 1 mm, the ovary densely pubescent, the 3 styles glabrous to sparsely pubescent; bisexual flowers with the stamens to 3 mm long, about as long as the ovary, the ovary ellipsoid, 3-angled, densely grayish appressed-pubescent, the style 3-branched from near the base, its branches sparsely pubescent. *Fruits* red, stipitate, broadly obovate and emarginate to truncate at the apex, ca. 12 mm long, 1.2–2.5 cm wide, 3-celled, sparsely pubescent, usually prominently winged, the wing itself to 7 mm long, the valves densely tomentose within, the stipe to 3 mm long; seeds 1–3, enveloped at the base by a white aril.

The species is named in honor of A. M. Brenes, who made the first collection known to me. *Paullinia brenesii* is closest to *P. fuscescens* but is distinguished by its larger leaves and more broadly winged fruit.

Paullinia brenesii flowers in Panama in August and September. Fruits mature during November and December and probably also in January.

The species occurs in Honduras, Costa Rica, and Panama from sea level to 1,650 m. In Panama it is known only from lower montane rain forest in the vicinity of Boquete.

CHIRIQUÍ: Cerro Horqueta, 1650 m, *Croat 26906* (CAS, COL, CR, DUKE, F, GH, K, MEXU, MO, NY, P, PMA, RSA, TEX, U, US, VEN), *27025* (MO). Monte Rey above Boquete, *Croat 15720* (MO); *Croat & Porter 15674* (MO). NNE of Boquete, *Wilbur & Luteyn 19261* (DUKE).

6. **Paullinia bristanii** Croat.[11] TYPE: Panama, *Bristan 1165* (MO-2066160, holotype).

Lianas; stems deeply 3–6-sulcate, glabrous; wood simple. *Leaves* pinnately 5-foliolate, 14–32 cm long, glabrous except for the vein axils beneath; petiole 2.5–10 cm long; petiole and rachis with a prominent medial rib on the upper surface, narrowly winged throughout, the wings slightly broader near the apex; leaflets elliptic, ovate-elliptic or obovate-elliptic, abruptly acuminate at the apex, attenuate to acute or obtuse at the base, 5–16 cm long, 2–7 cm wide, entire or weakly and obscurely toothed near the apex, drying dark; stipules deciduous. *Inflorescences* spikelike, axillary, more than 4 cm long, the rachis prominently angular, densely tomentulose, the bracteoles narrowly linear-lanceolate, 3–5 mm long, densely pubescent on both surfaces; pedicels short, shortly appressed-pubescent. *Flowers* unknown; sepals (persisting in fruit) to 2 mm long, sparsely appressed-pubescent outside, glandular within. *Fruits* globose, sessile, glabrous; immature fruit to ca. 1 cm diam.

The species is easily confused with *P. sternii* but can be distinguished by its globose, glabrous fruit.

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[11] *Paullinia bristanii* Croat, sp. nov. Labrusca fruticosa, corpus lignosum simplex. Folia 5-foliolato-pinnata; petiolus rhachisque anguste alata omnino. Inflorescentia axillaris, spiciformis, plus quam 4 cm longa. Fructus globosus, sessilis, glaber.

Paullinia bristanii is known only from the type collection. It is named in honor of Narciso Bristan, the able Panamanian plant collector and former assistant for James Duke during his years of collecting in Panama. The type has immature fruits and was collected in July.

DARIÉN: Río Ucurgantí, *Bristan 1165* (MO).

7. **Paullinia buricana** Croat.[12] TYPE: Panama, *Croat 21979* (MO-2195672, holotype; F, PMA, US, isotypes).

Lianas; stems 3-sided when young, sparsely hispidulous to villous, viscidulous, glabrous and terete in age; wood simple. *Leaves* ternate-pinnately compound, 8–25 cm long, 11-foliolate, the lowermost set of leaflets biternate with two additional sets of leaflets; petioles without wings, 1.5–4.5 cm long, prominently canaliculate above, the upper margins of the petiole and medial ridge of the rachis coarsely pubescent; lower rachis margined, the upper rachis margined or narrowly winged especially toward the apex; leaflets oblong-lanceolate to narrowly elliptic or ovate-lanceolate, sharply acuminate or rarely acute to rounded at the apex, attenuate to acute at the base, 2.2–12 cm long, 1–4.2 cm wide, entire or nearly so, somewhat shiny and glabrous but scabrid on the prominently raised upper midrib and on the major veins below, the vein axils often barbulate beneath, the major lateral veins 5–8 pairs, faintly loop-connected near the margin; stipules linear-lanceolate, brown, 5–10 mm long, glabrous except for the long-ciliate margins. *Inflorescences* of usually 2-several (rarely 1), slender thyrses 5–10 cm long, at least sometimes at leafless nodes; rachis puberulous; bracteoles narrowly lanceolate-linear, pubescent, to 1 mm long; pedicels 0.5–1.5 mm long, puberulent. *Flowers* greenish white; outer sepals puberulent, ciliate, 1.5–2 mm long; petals oblong-obovate, to 3.5 mm long, the scales nearly as long as the petals, the basal part elliptical, ca. 1.3 mm long, long-ciliate, the crest linear, much longer than the basal part, glabrous, the deflexed appendage densely bearded throughout, the lateral scales also bearing a simple linear crown; disc glands 4, subequal, small, closely clustered, puberulent on the inner surface; staminate flowers with the stamens to 2.5 mm long, the filaments villous, flattened, united briefly at base, the pistil minute, the ovary sharply trigonous, very sparsely hispid on the margins; bisexual flowers unknown. *Fruits* unknown.

The species is distinguished by its ternate-pinnate, almost glabrous leaves with petioles without wings, narrowly winged rachises, and slender fasciculate thyrses. Flowers are unusual in having a single linear scale crown.

Paullinia buricana apparently flowers in the dry season. It is known only from the type collected in an isolated area of tropical wet forest in a low lying region of westernmost Panama.

CHIRIQUÍ: 10–11 mi W of Puerto Armuelles, 400–600 m, *Croat 21979* (F, MO, PMA, US).

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[12] *Paullinia buricana* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex. Folia ternato-pinnata, 11-juga, fere glabra; petiolus nudus; rhachis marginata. Thyrsi graciles, 5–10 cm longi, fasciculati. Flores squama singulari lineari. Fructus ignotus.

8. **Paullinia correae** Croat.[13] TYPE: Panama, *Dwyer & Gentry* 9398 (MO-2172158, holotype; NY, PMA, isotypes).

Lianas; stems terete, densely yellowish-hispid when young, glabrate in age, purplish and weakly viscidulous; wood simple. *Leaves* usually biternate, with one or both of the ternate lower pairs sometimes simple, the leaf then pinnately 5-foliolate (or rarely 3-foliolate), 12–30 cm long, sparsely hispid throughout on both surfaces; petiole 1.5–6 cm long, without wings; rachis conspicuously winged, the wing 5–9 mm wide; leaflets oblong-elliptic to narrowly ovate or oblanceolate, acuminate or less commonly acute at the apex, attenuate to acute at the base, 3.5–18 cm long, 1.5–7 cm wide, coarsely crenate-serrate above the middle; stipules lanceolate-linear, ca. 1 mm wide at the base, sparsely hispid, 8–12 mm long. *Inflorescences* densely clustered in inconspicuous, few-flowered fascicles on leafless stems; pedicels inconspicuously pubescent. *Flowers* sessile or nearly so, white; sepals glabrous, the outer to 1.8 mm long, the inner ca. 3.2 mm long; petals narrowly oblong-obovate, to 3.5 mm long, little more than 1 mm wide, glabrous except for the sparsely long-ciliate margins, glandular within, the anterior scales nearly as long as petals, elliptic, glabrous except for the long-ciliate margin; crest deeply bifid, orange, the deflexed appendage glabrous except for the sparsely long-ciliate margin, orange, shorter than the crest, the lateral scales with the crest simple; disc glands nearly oblong, glabrous; stamens with the filaments sparsely long-pubescent; bisexual flowers with the stamens to 2 mm long, the pistil to 2.5 mm long, the ovary ovoid, 3-sided, sparsely hispid on the angles, the style as long as the ovary, 3-branched in the upper half. *Fruits* almost rounded, red, prominently 3-winged, emarginate, truncate to rounded at the base, 1.5–2.2 cm long, 1.8–2.5 cm wide, 3-locular, glabrous outside with prominently raised nerves, yellowish wooly-tomentose inside, the wing 3–7 mm wide; seeds 1 or 2, globose, black, shiny, conspicuously grayish-velutinous, ca. 7 mm diam.

Paullinia correae is distinguished by its terete stems (glabrate in age) with simple wood, usually biternate, hispid leaves and small, glomerulate inflorescences with 3-winged fruits. The species is most closely related to *Paullinia hispida* Jacq. of South America but differs from that species by its narrow stipules and less compounded blades. The leaves of *P. hispida* are 2–3 times compounded with the lower pairs of pinnae at least 5-foliolate. Its stipules are ovate to rounded or cordate. In Panama, *P. correae* is most easily confused with *P. baileyi*, but it is distinguished from that species by its smaller flowers, smaller inflorescences, usually biternate leaves (versus always 5-foliolate in *P. baileyi*), and terete stems. The stems of *P. baileyi* are larger and consistently deeply 4- or 5-sulcate. Other differences between the two species are the size and shape of fruits and the shape of the scale crown of the anterior petals.

Paullinia correae is named in honor of its first collector, Mireya Correa A., curator of the herbarium at the University of Panama. It flowers in the mid-

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[13] *Paullinia correae* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex; caules teretes. Folia plerumque biternata, sparsim hispida omnino. Inflorescentia dense fasciculatae thyrsis pauci-floriferis inconspicuis in caulibus aphyllis. Fructus globosus, manifeste trialatus, 1.5–2.2 cm longus.

rainy season in September and October; flower buds are seen as early as July. Fruits mature from December through April.

The species is known only from central Panama in tropical wet forest near the Canal Zone.

COLÓN: Santa Rita Ridge, *Correa 1091* (MO, PMA). Santa Rita Ridge, *Croat 15346* (MO); *Dwyer & Gentry 9398* (MO, NY, PMA); *Gómez-Pompa et al. 3157* (MO). PANAMÁ: Cerro Jefe, *Dwyer & Gentry 9490* (MO); *Gentry 4889* (MO); ca. 1000 m, *Gentry 6134* (MO, SCZ), *6769* (GH, MO).

9. **Paullinia costaricensis** Radlk., Serj. Suppl. 157. 1886. TYPE: Costa Rica, Cartago, *Oersted 6660* (C).

Serjania pubescens Seem. f. *glabrescens* Seem., Bot. Voy. Herald 92. 1853. TYPE: Panama, *Seemann 1642* (BM, K).

Tendrilled *lianas*; stems terete, usually densely villous; wood simple. *Leaves* biternate, 5–11 cm long; petiole without wings, densely villous, 1–3 cm long; rachis narrowly winged, sometimes slightly broader above the middle, 1.5–2.5 mm wide; leaflets elliptic-lanceolate or rhombic, acute or rounded and apiculate at the apex, attenuate to rounded at the base, 1.5–8 cm long, 1–4 cm wide, membranous, glabrous or nearly so on the upper surface, usually pubescent on the raised major veins, sparsely or densely villous beneath or almost glabrous except on the major veins, densely barbulate in the vein axils, prominently lobate-crenate, the teeth often glandular; stipules minute. *Thyrses* narrow, solitary in the leaf axils or clustered at the apex of stem, 10–15 cm long, densely puberulous; bracteoles minute. *Flowers* white; sepals ovate-elliptic, densely long-tomentose outside, glabrate inside, 2–3 mm long, 2–2.5 mm wide; petals oblong, 2–3 mm long, the scale on the inside of the petal ⅔ as long as the petal, crest short, suborbicular, emarginate, the deflexed appendage long-barbate; stamens with filaments flattened, sericeous, the anthers glabrous. *Capsules* long-stipitate, 3-locular, subglobose, puberulent, red, ca. 1 cm wide, prominently beaked, the stipe 4–5 mm long; seeds 1–3, globose, glabrous, black, shiny, 5–7 mm long, the aril white, covering the lower ⅓ of the seed.

The species is easily confused with *Paullinia fuscescens* var. *fuscescens*, but in Panama it can be distinguished vegetatively from that species by its commonly rhombic, more deeply lobate-crenate leaflets. Fertile plants are distinguished by flower clusters more distantly spaced on the inflorescence and by the subglobose, stipitate, beaked fruit without wings.

The phenological behavior of the species is uncertain. Plants which are definitely this species have had mature fruits in April. However, plants believed to be this species were in bud in August. The latter, represented by *Gentry* 5682, are from premontane wet forest at an elevation of 1,000 m and possibly are another species. Otherwise the species is known only from tropical moist forest in Panama.

The species is known from Guatemala to Panama. Collections from Mexico which are otherwise similar have leaves that are merely pinnate.

CANAL ZONE: Madden Dam, *Dwyer & Robyns 10* (MO, SCZ). 1 km W of Gamboa, *Nee 9444* (CAS, DUKE, GH, MO, NY, P, PMA, US, VEN). CHIRIQUÍ: 20 km N of Puerto Armuelles, *Busey 406* (CAS, MO, PMA, US). Remedios, *Seemann 1642* (BM, K). COCLÉ: El Valle, ca. 650 m, *Croat 25278* (MO). Above El Valle, ca. 1000 m, *Gentry 5682* (MO). COLÓN: Santa Rita Ridge, *Dwyer & Gentry 9518* (MO, NY, SCZ). PANAMÁ: Cerro Campana, *Croat 14740* (MO); 780–875 m, *Croat 25211* (MO).

10. **Paullinia costata** Schlecht. & Cham., Linnaea 5: 216, no. 442. 1830. TYPE: Mexico, Hacienda de la Laguna, *Schiede & Deppe 442* (B, destroyed, MO, photo).

P. scarlatina Radlk., Bot. Gaz. (Crawfordsville) 16: 193. 1891. TYPE: Guatemala, Yzabal, Boca del Cajabon, 350 ft, *Donnell Smith 1662* (US).

Tendrilled *lianas*; stems terete, glabrous, striate and rusty brown with numerous minute lenticels; wood simple. *Leaves* pinnately 5-foliolate, 3–20 cm long; petiole without wings, canaliculate on the upper surface, 0.5–7 cm long; rachis wingless to narrowly margined; leaflets narrowly ovate to oblong-elliptic or oblong-lanceolate, acute to gradually acuminate at the apex, attenuate to rounded at the base, 4.5–12 cm long, 1.5–4.5 cm wide, coriaceous, glabrous except for a few trichomes in the axillary domatia on the lower surface, the margin entire to obscurely and remotely crenate in the distal half; petiolules 1–4 mm long; stipules inconspicuous. *Thyrses* in compacted, cylindrical, axillary or terminal, racemiform inflorescences to 11 cm long, the branches, pedicels and sepals canescent-tomentose; pedicels stout, 2–3 mm long, articulate in the lower third. *Flowers* ca. 4 mm long, large for the genus; sepals obovate, cup-shaped; petals narrowly obovate, ca. 4.5 mm long, glandular on both surfaces, the scales to 5 mm long with the basal part to 3 mm long, ca. 1.5 times longer than broad, villous on the margins, the anterior petals with the crest deeply bifid, 1.5–2 mm long, orange, each branch of the crest ca. 0.5 mm wide, the deflexed appendage deltoid, densely villous near the margins; disc glands about as wide as long, glabrous except at the base; stamens to 2.5 mm long, the filaments flattened, wooly-pubescent throughout and the trichomes covering the base of the anther; ovary ovoid, densely tomentose, to 3.5 mm long, the style and stigmas short and stout. *Capsules* subglobose or ellipsoid, red, 2.5–4 cm long, 2–2.5 cm wide, sparsely to moderately puberulous to glabrous in age, often beaked at the apex, usually gradually tapered to a basal stipe, often apiculate at the apex, sometimes markedly 3-ridged when young, 3-celled, the stipe 3–6 mm long, the valves densely wooly within; seeds (1–)2(–3), ellipsoid to subglobose, 8–20 mm long, black, shiny, glabrous, the lower half enveloped by a fleshy white aril.

The species is distinguished by its stiff, 5-foliolate, pinnate leaves with wingless petioles and wingless or very narrowly winged rachises, and blades which dry dark and are glabrous except for the axillary domatia. It may also be recognized by its large nearly globular fruits with three weak ridges. A collection from Cerro Jefe (*Dwyer 8497*) has conspicuously smaller leaves than average but is believed to be this species.

In Panama the species flowers from November to April, mostly during the dry season. Fruits mature from March to June.

Paullinia costata is known from Mexico to Panama along the Caribbean coast. It is also known from the Guianas. In Panama, it occurs in premontane rain forest and tropical wet forest.

COCLÉ: 3–4 km W of Santa Fe, 2500 ft, *Nee 11286* (F, MO, PMA, RSA). PANAMÁ: Cerro Jefe, *Dwyer 8497* (MO). El Llano-Cartí Road, 10.8 km from highway, 1100–1200 ft, *Mori & Kallunki 4147* (MO, PMA, US). El Llano-Cartí Road, 20.7 km from Interam. Hwy., *Mori & Kallunki 5118* (F, MO, PMA). El Llano-Cartí Road, 8–12 km N of El Llano, ca. 400 m, *Nee et al. 8794* (MO, PMA, US). El Llano-Cartí Road, 8 km N of Pan-Am. Hwy., ca. 450 m, *Nee & Warmbrodt 10329* (F, MO, NY, PMA, US).

11. **Paullinia cururu** L., Sp. Pl. 365. 1753. TYPE: not seen.

Tendrilled *lianas*; stems terete, glabrous and shiny; wood composite. *Leaves* ternate, 8–20 cm long; petiole winged; leaflets elliptic or elliptic-lanceolate, usually acuminate at the apex, sometimes acute or obtuse, sessile or with a petiolule ca. 1 mm long, acute to attenuate at the base, 4–14 cm long, 1.6–5.5 cm wide, glabrous, membranous, the vein axils densely barbulate beneath, the margin denticulate in the distal portion. *Thyrses* solitary in the axils of the leaves; bracteoles subulate, 1.5 mm long. *Flowers* white, ca. 3 mm long; sepals rotund-ovate, tomentulose; petals oblong, acute, narrow at the base, the scale with villous margin, the crest emarginate and glabrous, the deflexed appendage broad and simply an extension of the scale with villous margins; stamens with the filaments filiform, sparsely pilose; ovary obovoid, 3-lobed. *Fruits* usually prominently curved, 1-locular, 3-valved, 1.5–2.5 cm long, sparsely appressed-pubescent to glabrate, bright red; seed 1, 7–9 mm long, the aril white, fleshy.

The species is distinguished by its 3-foliolate leaves with winged petioles and by its prominently curved, red capsules.

Flowers are apparently ephemeral and are seldom found on specimens. Fruits mature May to October but especially in July.

The species ranges from Mexico to Colombia, Venezuela, Brazil, and the West Indies. In Panama it is mostly restricted to the Pacific coast, but it is ecologically variable, occurring principally in disturbed forest edges of tropical moist forest. It also occurs in tropical dry forest and premontane wet forest.

CANAL ZONE: Vic. TTC Albrook tower, *Blum 1214* (MO, SCZ). C-15 Road, *Blum & Dwyer 2453* (MO, PMA). Madden Dam, Boy Scout Camp Road, *Dwyer 7511* (MO). Vic. of Fort Sherman, *Standley 30979, 31152* (both US). Vic. of Salamanca Hydrographic Station, Río Pequení, 80 m, *Woodson et al. 1561* (GH, MO, NY, US). CHIRIQUÍ: E of Gualaca, *Allen 5028* (F, MO, U). COCLÉ: Hills S of El Valle, *Allen 2517* (MO, NY, US). DARIÉN: Río Chucunaque near Río Tuquesa, *Stern et al. 951* (GH, MO, US). HERRERA: Ocú, *Ebinger 1066* (F, GH, MO, US). PANAMÁ: Vic. of Río Pacora on Pan-Am. Hwy., *Bartlett & Lesser 16947* (MICH, MO). 5 mi N Cerro Azul, *Blum et al. 1693* (DUKE). Nueva Gorgona, *Duke 4509* (GH, MO, US). Near Río Mar, 5–20 m, *Duke 12415* (MO, US). Isla Pedro Gonzales, *Dwyer 1748* (MO). Taboga Island, *Gentry 5721* (MO, U). Near Tapia River, *Maxon & Harvey 6621* (US). E of Bella Vista, *Maxon & Valentine 6965* (C, US). Saboga Island, Perlas Island, *Tyson 5600* (DUKE, MO, SCZ). Río Mar, *Tyson et al. 2308* (SCZ). Río Tataré, *Woodson & Schery 1019* (MO, US). Isla Taboga, *Woodson et al. 1536* (GH, MO, NY, US). VERAGUAS: Santiago, *Dwyer & Kirkbride 7414* (MO). 12 mi from Santiago toward Divisa, *Dwyer & Kirkbride 7431* (MO). WITHOUT EXACT LOCALITY: *Hayes s.n.* (BM).

12. **Paullinia dasystachya** Radlk., Monogr. Paull. 270, no. 95. 1895–1896. LECTOTYPE: Bolivia, *Bang 2815* (C, F, G, K, MO, NY, W, Z).

P. acutangula Britt., Bull. Torrey Bot. Club 16: 190. 1889, non Pers., 1887. TYPE: Bolivia, *Rusby 531* (not seen).

Lianas or scandent *shrubs* to 3 m tall; stems weakly viscidulous, terete or weakly ribbed, sparsely to densely brownish hirtellous-tomentose; wood simple. *Leaves* pinnately 5-foliolate, 15–30 cm long; petiole terete, 2.5–6 cm long; rachis terete; both petiole and rachis densely rufous hirtellous-tomentose; leaflets sessile or short-petiolulate, ovate to elliptic or obovate, acuminate to acute at the apex, attenuate to rounded at the base, (3–)6–14 cm long, (1.5–)3.5–8.5 cm wide, coarsely serrate-dentate mostly above the middle with glandular teeth, the surfaces glistening, sparsely hirtellous above, the pubescence denser on the veins, beneath hirtellous to pilose especially on the veins; stipules lanceolate, to ca. 5 mm long, densely hirtellous on the outer surface, glabrous inside. *Inflorescences* axillary or terminal on new growth or borne on tendrils; thyrses solitary, 3–14 cm long, densely rufous hirtellous-tomentose throughout; bracteoles similar to the stipules but smaller, to ca. 3 mm long; pedicels densely long-pubescent, ca. 1 mm long. *Flowers* (Bolivian material) white; outer sepals ovoid, to 2.5 mm long, densely pubescent outside, ciliate, glabrous inside, the inner sepals obovate, to 4 mm long, sparsely pubescent outside, minutely ciliate, glandular inside; petals narrowly obovate, glandular, the anterior scales ca. ¾ as long as the petals, the basal part as broad as long, densely ciliate, the crest deeply bifid, orange, ca. 1.2 mm long, the deflexed appendage broadly rounded, glabrous except on the extreme margins, shorter than the crest; disc glands 2, semicircular, densely long-pubescent, almost hidden by the pubescence of the disc; stamens with the filaments flattened, densely villous throughout; staminate flowers with stamens to 4 mm long, the filaments united at the base, the pistil minute, densely silky-pubescent; bisexual flowers not seen. *Fruits* obovate, truncate and apiculate at the apex, acute to attenuate at the base, 3-winged, stipitate, to 2.5 cm long (including stipe), red, densely brownish hirtellous-tomentose outside, white hirtellous-tomentose within, the wings broadest toward the apex, the stipe ca. 5 mm long; seed 1, subglobose, ca. 7 mm diam., black, shiny, glabrous, white-arillate at the base.

Paullinia dasystachya is recognized by its 5-foliolate leaves with densely hirsute-tomentose, terete petioles and rachises.

The species was previously known only from Ecuador, Peru, Brazil, and Bolivia. It has been collected once in Panama in a region bordering tropical moist forest and premontane moist forest. This fruiting collection was made in the dry season.

HERRERA: 2 mi NW of Ocú, *Stern et al. 1696.*

13. **Paullinia dodgei** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 642. 1937. TYPE: Costa Rica, San José Prov., low hills over Río Paquita, 5–50 m, *Dodge & Goerger 9877* (F, holotype; MO, isotype).

Lianas; stems terete, fulvous-pilose when young, glabrous in age, often densely lenticellulate; wood simple. *Leaves* pinnately 5-foliolate, 13–35 cm long; petiole 3–10 cm long, without wings, canaliculate above; petiole, rachis and both leaf surfaces fulvous pilose; rachis winged, the wing 2–4 mm wide; leaflets elliptic to oblong-elliptic (the terminal one obovate-elliptic), sharply long-acuminate at the apex, attenuate to obtuse at the base, 7–19 cm long, 3–6.5 cm wide, thin, with 3–5 conspicuous dentate-serrate teeth on each side; stipules linear, to ca. 1 cm long, sparsely hispid throughout, weakly viscidulous. *Inflorescences* borne on defoliated stems, the thyrses borne singly or usually in fascicles on an elevated part of the stem, 3–18 cm long, slender, densely strigose and hispid; bracteoles linear, 3–8 mm long, sparsely hispid along the margins; pedicels slender, 2–3 mm long, appressed-pubescent. *Flowers* white, to 3 mm long and 6 mm wide; sepals broadly rounded, finely and densely appressed-puberulent, broadly spreading at anthesis; petals obovate, the anterior scales ¾ as long as the petals, elliptical, the deflexed appendage short, sparsely pubescent, the crest obovate, the scales of the lateral petals consisting of a simple fold, densely to sparsely white-ciliolate, sparsely pilose on the face, the crest simple to emarginate, weakly puberulent inside; disc glands ovate to oblong, 0.7 mm long, densely appressed puberulent throughout; bisexual flowers with stamens ca. 2 mm long, the filaments flattened, glabrous on the outer surface, villous within, the ovary ovoid, ca. 1 mm long, densely appressed pubescent, the style ca. 1 mm long, 3-branched more than half its length. *Capsules* narrowly obovoid, apiculate at the apex, narrowly acute at the base, to 2.3 cm long and 1 cm wide, 3-sided, moderately appressed-puberulent, red.

The species is recognized by its pinnately 5-foliolate, pilose leaves, winged rachises, fasciculate slender thyrses, and pilose young stems, petioles and rachises.

In Panama flowering occurs in the rainy season from June through October. Fruits develop to mature size by September but the time of fruit maturity is unknown.

Paullinia dodgei is known only from Costa Rica and Panama. In Panama it is known from tropical moist, premontane wet and tropical wet forests.

DARIÉN: La Boca de Pirre, *Bristan 1252* (MO). Cerro Pirre, 100–600 m, *Duke 5289* (GH, MO). Ca. 1 mile SE of Río Tuira, *Duke 14565* (MO). Vic. of Yaviza, *Stern et al. 131* (GH, MO). PANAMÁ: Halfway between El Llano and Río Mamoní, *Duke 5589* (MO). El Llano-Cartí road, 9.6 km from highway, 410 m, *Mori & Kallunki 1858* (MO, PMA). SAN BLAS: Ailigandí River, *Duke & Bristan 328* (MO, US).

14. **Paullinia dukei** Croat.[14] TYPE: Panama, *Duke 14621* (MO-2209208, holotype).

Lianas; stems 4- or 5-sulcate when young, granular-puberulent, glabrate and terete to obscurely 3-angled in age; wood simple. *Leaves* 15–30 cm long, pinnately

[14] *Paullinia dukei* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex. Folia 5-foliolata-pinnata; foliola 6.5–11.5 cm longa, 2.2–3.2 cm lata, remota-crenata-serrata supra medium; petiolus rhachisque nuda. Thyrsus elongatus, solitarius, axillaris, 10–12 cm longus. Fructus obovatus vel anguste obovatus, 2.5–3.5 cm longus, sessilis aut bevi-stipitatus; semina 2.

5-foliolate (rarely 3-foliolate); petioles terete, margined, weakly viscidulous, granular-puberulent, 7–11 cm long; rachis terete, margined; leaflets elliptic or lanceolate-elliptic to oblong-elliptic or narrowly ovate, long-acuminate at the apex, acute to narrowly rounded at the base, 6.5–20 cm long, 2.2–6.8 cm wide, weakly viscidulous, entire or remotely crenate-serrate above the middle, glabrous above except for the puberulent, prominently raised midrib, glabrous beneath except for the puberulent to hispidulous midrib and base of the lateral veins, more prominently pubescent in the vicinity of the vein axils, the major lateral veins 8–10 pairs, prominently raised beneath, sometimes joining the gland-tipped teeth at the margin. *Inflorescences* thyrsiform (fruit), granular-puberulent; bracteoles lanceolate-linear, sometimes bearing a tendril, to ca. 1.5 mm long. *Flowers* not known. *Fruits* obovoid to narrowly obovoid, 2.5–3.5 cm long, brown maroon (fide Duke), without wings, rounded to obtuse or shortly beaked at the apex, acute at the base, sessile to short-stipitate, glabrous, the valves striate, ca. 3 mm thick when dried, glabrous within; seeds 2, 1.3–1.7 cm long, elliptic in side-view, rounded on the outer surface, the inner surface sometimes forming an obtuse angle.

The species is named in honor of its collector James A. Duke. It is distinguished by its wingless 5-foliolate leaves and solitary axillary thyrses with wingless, obovoid, closely striate fruits.

The species has been collected in fruit in October and November. The fruits are reportedly eaten by toucans (*Duke 14621*).

The species is known only from tropical moist forest in Darién Province and premontane wet forest at an elevation of 800 m in Panamá Province.

DARIÉN: Río Tuira, between Río Penusa and Río Mangle, *Duke 14621* (MO). PANAMÁ: 5 mi N Cerro Azul, *Blum et al. 1693* (DUKE, SCZ).

15. **Paullinia eliasii** Croat.[15] TYPE: Panama, *Croat 26166* (MO-2205213, holotype; K, PMA, US, isotypes).

Lianas, leafless near the ground; stems terete to 3-sided when young, the older stems terete or more commonly deeply 3-sulcate, in age the stem becoming so deeply sulcate as to cause the 3 terete segments to become nearly free; wood simple. *Leaves* pinnately 5-foliolate, nearly glabrous; petioles narrowly winged especially toward the apex, 3.5–7 cm long; rachis narrowly winged, the petiole and rachis pubescent on the midrib and scabridulous on margins of the wings; leaflets narrowly ovate, narrowly elliptic or oblanceolate, mostly long-acuminate, rarely obtuse at the apex, attenuate to obtuse at the base, 5–16 cm long, 1.5–5.5 cm wide, entire or remotely crenate-serrate with glandular teeth, glabrous above except for the midrib, glabrous beneath except for the densely barbulate vein axils, the margins scabridulous; stipules linear-lanceolate, 3–6 mm long, pubescent,

[15] *Paullinia eliasii* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex; rami plerumque profunde trisulcati aetate provecta. Folia 5-foliolata-pinnata; petiolus rhachisque anguste alata; foliola integra aut remota-crenata-serrata dentibus glandulosis. Inflorescentia gracilis, plerumque sine ramis, glomerulata, in ramis veteribus. Fructus obovatus, sine alis, stipitatus.

deciduous. *Inflorescences* borne on stout tubercles arising from the central cortex, the thyrses usually long, slender, clustered but few, mostly simple, rarely branched, appressed-puberulent to tomentulose, viscidulous, to ca. 15 cm long; pedicels appressed-pubescent, to 2.5 mm long, articulate below the middle. *Flowers* white; outer sepals appressed-puberulent, rounded, to 2 mm long, the inner sepals obovate, inconspicuously short-puberulent; petals obovate, to 2.8 mm long, the anterior scales ⅔ as long as the petals, the lower part as broad as long, long-ciliate, conspicuously pubescent on the inner surface, glabrous on the outer surface, the crest short-obovate, truncate to emarginate, pale orange, the deflexed appendages densely villous near the inner margins; disc glands 2, acute, densely villous throughout, the lateral scales consisting of a simple fold, the crest simple; staminate flowers with the stamens to 2 mm long, the filaments densely villous throughout, the pistil minute, densely pubescent at the apex. *Fruits* obovoid, beaked at the apex, gradually tapered toward the basal stipe, ca. 2.5 cm long, red, without wings, appressed-pubescent to glabrate, 3-locular, 2- or 3-seeded, the stipe ca. 5 mm long; seeds ovoid, 7–8 mm diam., pubescent, white-arillate at the base.

The species is named for Thomas S. Elias, one of several recent collectors. It is recognized by its 5-foliolate leaves with narrowly winged petioles and rachises, sharp glandular-toothed leaflets, slender, mostly unbranched, glomerulate inflorescences borne on the older stems, and turbinate, wingless fruits. Also of diagnostic value are the deeply 3-sulcate stems with simple wood.

Flowering occurs from June through September. Fruits develop to mature size by November and mature during the dry season from December to March.

Paullinia eliasii is known only from Panama in tropical wet forest and premontane rain forest.

COCLÉ: N rim of El Valle, *Woodson & Schery 163* (MO). COLÓN: Along Río Guanche, 3–5 mi inland, 10–100 m, *Croat 26166* (K, MO, PMA, US). Río Guanche, 1–4 km upstream, *Gentry 8808* (MO, PMA, US). Santa Rita Ridge Road, *Mori & Kallunki 1803* (F, MO, PMA), *3028* (MO). Río Guanche, ca. 2.5 km upstream, 10–100 m, *Mori & Kallunki 3704* (MO, PMA, US). Santa Rita Ridge Road, *Mori & Kallunki 4906* (MO). DARIÉN: Cerro Pirre, *Duke & Elias 13852* (MO). PANAMÁ: Cerro Jefe, *Dwyer & Gentry 9441* (MO). Gorgas Memorial Labs Yellow Fever Research Camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki 3361* (MO, PMA, US).

16. **Paullinia faginea** (Triana & Planch.) Radlk., Monogr. Serj. 76, no. 142. 1875.

Enourea faginea Triana & Planch., Ann. Sci. Nat., sér. 4., 18: 379. 1862. TYPE: Colombia, *Triana 3463* (BM, F, G, K, NY, P).
Paullinia elongata Radlk., Monogr. Paull. 238. 1895. TYPE: Peru, Huanuco, Vitoc, *Ruiz & Pavon* (G, not seen, MO, photo).
P. florenciana Cuatr., Revista Acad. Colomb. Ci. Exact. 4: 347. 1941. TYPE: Colombia, Comisaria del Caqueta, Florencia, 400 m, *Cuatrecasas 8818* (US).

Lianas; stems terete, densely rufous-tomentose when young, not obviously pubescent on second year growth; wood simple. *Leaves* pinnately 5-foliolate, 5–37 cm long, sparsely rufous-pubescent on the petioles, rachises and petiolules; petiole and rachis terete; petioles 4.5–12 cm long; petiolules 2–10 cm long; leaflets elliptic, oblong-elliptic, ovate-elliptic or obovate-elliptic, acuminate at the apex, the acu-

men sometimes prolonged 1.5 cm, acute to obtuse at the base, 6–21 cm long, 3–7 cm wide, crenate-serrate especially in the distal half, the teeth usually glandular, the upper surface glabrous except on the veins, the lower surface glabrate except on the veins (often more densely pubescent in South America), the major lateral veins mostly 12 pairs, prominent beneath and markedly regular, the tertiary veins, prominulous, extending all the way between the major laterals; stipules conspicuously elliptic-lanceolate, ca. 1 cm long. *Thyrses* solitary in the leaf axils, borne on tendrils or arranged in panicles, stout, elongate and unbranched, to 25 cm long; pedicels 1.5–2 mm long, articulate above the middle. *Flowers* (Colombian collections) white; sepals to 3 mm long, rufous-tomentose outside; petals oblong-rounded, ca. 2 mm long, about ⅔ as wide as long, rounded at the apex, glabrous outside, sparsely glandular within, the scale about ¾ as long as and as wide as the petal, markedly cup shaped, glabrous except densely pilose along the margins, the deflexed appendage short, densely white-bearded, the crest of 2 flattened, imbricate, ear-shaped lobes slightly longer than broad; disc glands glabrous except at the base, as broad as long; stamens glabrous at the base, densely villous above the middle, flattened; staminate flowers with the stamens to 2 mm long, the pistil 1 mm long, densely pubescent at the base. *Capsules* globose, ca. 2.5 cm diam., yellowish brown pubescent, the valves ca. 2 mm or more thick.

Paullinia faginea is recognized by its 5-foliolate leaves with wingless petioles and rachises and densely reddish brown, tomentose, simple stems. It is markedly similar to both *P. fraxinifolia* Triana & Planch. and *P. macrocarpa* Radlk. from Colombia, but both of those species are described as having markedly ribbed stems. It is also similar to *P. firma* Radlk. from Brazil.

Phenological behavior of the species is poorly known. Costa Rican collections have flowers in May and July but the species has also been collected in Colombia with flowers in December and mature fruits in May.

The species ranges from Costa Rica to Peru. In Panama it is known from tropical wet forest.

CHIRIQUÍ: Santa Clara region, 27 km NW of El Hato del Volcán, 500–5300 ft, *Mori & Bolton 7454* (MO, PMA). PANAMÁ: El Llano-Cartí Road, 10.8 km from Interam. Hwy., 1100–1200 feet, *Mori & Kallunki 4147* (MO). VERAGUAS: 11 km beyond Santa Fe, 650 m, *Croat 25642* (MO).

17. **Paullinia fasiculata** Radlk., Monogr. Paull. 124. 1895–1896. TYPE: Guiana, *Poiteau* (G).

Lianas; stems sharply triangular when young, glabrate, becoming markedly 3-ribbed in age and sometimes appearing as 3 separate strands only loosely attached; wood composite with an irregular central core and three smaller peripheral bundles, these separating in age, the periderm coarse, somewhat exfoliating in age. *Leaves* pinnately 3–5-foliolate; petioles 3–13 cm long, narrowly winged, glabrous or scabridulous at the apex and sparsely so along the margins of the wings; rachis of the 5-foliolate leaves winged, the wing similar to the petiole wing; leaflets elliptic to ovate- or oblong-elliptic, gradually to abruptly acuminate to

acute at the apex, acute to obtuse at the base, 7–20 cm long, 3–9 cm wide, glabrous or puberulent only on the midrib above, glabrous beneath except for some barbulate vein axils, the margins sparsely scabrid, the reticulate veins prominulous on both surfaces; juvenile leaves simple, 15–25 cm long, 8–14 cm wide; stipules linear-lanceolate, 3–4 mm long, striate, glabrous inside, appressed-pubescent outside, often deciduous. *Inflorescences* of densely glomerulate thyrses borne on raised protuberances from the central strand of the stem; rachis branched, to ca. 2 cm long; rachis, pedicels, and calyces sparsely appressed-puberulent to glabrate, drying dark brown; bracteoles narrowly triangular, less than 1 mm long; pedicels to ca. 6 mm long. *Flowers* sweetly fragrant, white; buds broadly oblong, somewhat flattened laterally; outer sepals 1.5–2 mm long, ellipsoid, sparsely appressed-pubescent outside, glabrous within, the inner sepals obovate, appressed-puberulent outside, glabrous within; petals oblong-obovate, 3–4.5 mm long, the scales ⅔–¾ as long as the petals, the basal part rounded, 1.5 mm long, glabrous or with the margin sparsely ciliate, the crest obovate to inequilaterally emarginate, thin, orange, the deflexed appendage shorter than or equalling the crest, rounded at the base, glabrous or densely villous; disc glands white, semicircular or longer than broad, puberulent to appressed-puberulent in at least the lower half within; stamens with the filaments flattened, loosely villous in the lower half; staminate flowers with the stamens basally united, to ca. 3 mm long, the pistil minute, appressed-pubescent on the upper half of the ovary and on the style and stigmas; bisexual flowers with the stamens ca. 1.8 mm long, free, the ovary and style together 3.5 mm long, the ovary 1.5 mm long, densely pubescent, the style 3-branched in the upper ¼, sparsely pubescent. *Capsules* obovoid-pyriform, long-stipitate, 1.5–2 cm long, apiculate and obscurely 3-winged at the apex, the outer surface sparsely short-pubescent toward the apex, glabrous toward the base, longitudinally striate, the inner surface apparently glabrous.

The species is distinguished by the (3–)5-foliate leaves with winged petioles and rachises, glomerulate inflorescences with small acute bracts, rachises much longer than pedicels, and 3-sulcate stems with composite wood.

In Panama flowering occurs from December to February with fruits developing during April and May.

Paullinia fasciculata ranges from Costa Rica to Panama. It is also known from Guyana and Tobago (West Indies). In Panama it occurs principally in premontane wet forest and tropical wet forest but also in wetter parts of tropical moist forest on the Atlantic slope.

BOCAS DEL TORO: Daytonia region of Almirante, *Cooper 135* (F). COLÓN: Lower Río Guanche, *Dressler 4238* (MO). S of Portobelo, *Foster 2065* (DUKE). Río Guanche, *Foster 2198* (DUKE); *Mori & Kallunki 3020* (MO, PMA); 0–10 m, *Nee & Gentry 8693* (CAS, F, MO, PMA, RSA, US). PANAMÁ: El Llano-Cartí Road, 8–12 km N of El Llano, 400–450 m, *Nee et al. 8767* (F, MO, PMA, US).

18. **Paullinia fibrigera** Radlk., Smithsonian Misc. Collect. 61(24): 2. 1914. TYPE: Panama, *Williams 672* (US).

Tendrilled *lianas*; stems terete except when very young, minutely puberulent and lenticellate; wood simple; sap milky, forming droplets near the periphery

of stems when seen in cross section. *Leaves* pinnately 5-foliolate, 8–40 cm long, glabrous except for puberulence on the upper side of the petiole, rachis and midribs, and the usually barbulate axils of the lower leaf surface; petiole to 10 cm long; petiole and rachis winged; leaflets oblong-elliptic to oblanceolate, obtuse to acuminate at the apex, obtuse at the base, 7–23 cm long, 3–9 cm wide, punctate on both surfaces, especially below, entire or sometimes with a single tooth on each side; stipules ovate, small. *Inflorescences* upper axillary, the thyrses slender, usually unbranched, to 12 cm long, to 25 cm long in fruit. *Flowers* white, to 3.5 mm long; sepals tomentulose, unequal, 2 reduced and 1 concave and partially enclosing the anterior petals; petals glabrous, to 3 mm long, weakly glandular on both surfaces, the scales shorter, the anterior petals with a deflexed appendage, villous throughout, the crest of the scale yellow, 2-lobed, the lobes slender; disc glands orange, semicircular, flattened, glabrous or puberulous; stamens with the filaments flattened, villous, weakly fused at the base, those of the bisexual flowers to 2.8 mm long; ovary ovoid, terete, densely tomentose, the styles short, stout. *Capsules* globose to broadly clavate, prominently beaked at the apex, gradually narrowed to a stipe, 1-locular, densely rufous-tomentose, to 2 cm long and 1.5 cm wide, the valves thin, the stipe 3–7 mm; seed 1, ellipsoid, laterally compressed, ca. 1.2 cm long.

The species is most easily confused with *Paullinia pinnata* but can be distinguished by its terete stems, densely rufous-tomentose fruits and mostly entire leaves. It is very similar to *P. pterophylla* Triana & Planch. based on a type photo of *Triana 3453*. Radlkofer reported *P. pterophylla* from Nicaragua and Colombia. The Triana collection differs in having up to nine leaflets instead of five and in having the leaflets markedly crenate toward the apex.

In Panama *P. fibrigera* flowers from September to November but mostly in October. Fruits mature in the early dry season, mostly in December and January. Old capsules persist on the plants for some time.

The species is known only from tropical moist forest in Panama but is to be expected in Colombia and Costa Rica.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 637* (F); *Croat 5672* (MO), *Croat 6062* (MO, SCZ), *6700* (MO), *6731* (DUKE, F, MO, NY, SCZ), *6765* (MO), *7341* (DUKE, F, MO, NY, SCZ), *11825* (MO), *12586* (DUKE, MO, NY, SCZ), *12841* (F, MO, NY, SCZ); *Foster 727* (DUKE, F, MICH, MO, PMA), *1131* (DUKE), *1298* (DUKE, F, MICH, MO, PMA), *1418A* (DUKE, MO, PMA); *Shattuck 520* (F, MO, US); *Wetmore & Abbe 217* (A, F, GH, MO). W Quebrada Salamanca, 70 m, *Dodge et al. 17000* (K, MO, P, S). Pipeline Road, *Gentry 1929* (MO, SCZ). Gatún, *Hayes 124* (NY). 4 km NW of Summit Garden, 70 m, *Nee 9057* (CAS, COL, CR, DUKE, F, GH, K, MICH, MISSA, MEX, MO, NY, P, PMA, RSA, TEX, US, VEN). Along Río Chagres, *Steyermark & Allen 16779* (G, MO, U). Below Río Indio Hydrographic Station, *Steyermark 17394* (G, MO, S, U). CHIRIQUÍ: Burica Peninsula, along Quebrada Tuco, *Croat 22099* (MO). DARIÉN: Manené to mouth of the Río Cuasí, *Kirkbride & Bristan 1484* (MO, NY). Cituro, *Williams 672* (US). PANAMÁ: Cerro Jefe, *Wilbur et al. 11355* (DUKE).

19. **Paullinia funicularis** Radlk., Smithsonian Misc. Collect. 61(24): 3. 1914. TYPE: Panama, *Pittier 3886* (US-678961, holotype; GH, M, isotypes).

Lianas; younger stems weakly viscidulous and sharply 3-sulcate, the ribs prominently canaliculate, their margins prominently yellowish-hirtellous, the

older stems prominently and irregularly 3-ribbed; wood simple. *Leaves* ternate-pinnately compound with 11 leaflets, to 25 cm long, the lowermost pair of segments biternate; petioles 2.5–9.5 cm long, without wings, prominently canaliculate above, the lower rachis margined or narrowly winged, the wing 2–3 mm wide, the upper rachis prominently winged, the wing 5–10 mm wide, broadest near the apex, the marginal ribs of the petioles as well as the medial ridge and wing margins of rachises densely long-hirsute; leaflets oblong-lanceolate or oblong-elliptic, abruptly acuminate or rarely acute at the apex, attenuate to acute at the base, 5–12 cm long, 2.5–4.7 cm wide, thin, crenate-dentate in the outer ⅔–½ with glandular teeth, sparsely hispid on the major veins beneath and on the margin and over the surface above, especially the midrib; stipules 1–2 cm long, prominently hispid-ciliate, otherwise glabrous. *Inflorescences* axillary, cauliflorous, or borne on tendrils, the thyrses often solitary when borne in the leaf axils and on tendrils, glomerulate on older stems; rachises branched, glabrate or sparsely pubescent; bracteoles lanceolate, long-ciliolate; pedicels to ca. 4 mm long; pedicels and sepals sparsely appressed-pubescent to glabrous. *Flowers* white; sepals elliptic, glabrous, the outer ca. 1.5 mm long, the inner to 4 mm long; petals oblong-obovate, 4–4.5 mm long, glandular within, the anterior scales about as broad as long, 2.2–2.5 mm long, ciliate, the crest obovate, shorter than the deflexed appendage, the latter densely ciliate marginally; disc glands 2, oblong, short-villous outside; staminate flowers with the stamens to 2.5 mm long, the filaments villous, flattened, fused near the base, the pistil densely appressed-pubescent; bisexual flowers with the stamens to 2.5 mm long, the pistil to 4 mm long, the ovary densely appressed-pubescent, ca. 1.5 mm long, the style sparsely pubescent in the lower half, 3-branched in the upper fourth. *Fruit* not known.

The species is most closely related to *Paullinia mallophylla*. In Panama flowering occurs in the rainy season from July to October.

Paullinia funicularis is known only from Panama where it has been collected in tropical wet forest and wetter parts of tropical moist forest in the eastern half of the country.

CANAL ZONE: Along dirt road to Chiva-Chiva town, *Correa 492* (DUKE). COLÓN: Along Río Fato, 10–100 m, *Pittier 3886* (GH, M, US), *4188* (M, NY, US). DARIÉN: Río Balsa, between Manené and Tusijuanda, *Duke 13581* (MO, PMA). SAN BLAS: Road between Mandinga and Cangandí, *Duke 14728* (MO, PMA).

20. **Paullinia fuscescens** H.B.K., Nov. Gen. Sp. Pl. 5: 93. 1821. TYPE: Brazil, Fl. Amazonas, *Humboldt & Bonpland* (P).

20a. **Paullinia fuscescens** var. **fuscescens.**

P. velutina DC., Prodr. 1: 605. 1824. TYPE: New Granada, *Bertero* (not seen).
Serjania pubescens Seem., Bot. Voy. Herald 92. 1853, non H.B.K., 1821. TYPE: Panama, Bay of Panama, *Seemann* 597 (BM, not seen).
Paullinia fusca Griseb., Bonplandia 6: 3. 1858. TYPE: Panama, *Duchassaing* (not seen).
Urvillea sinaloensis H. S. Gentry, nom. ined.

Tendrilled *lianas*; stems terete, pilose, usually not lenticellate, the younger stems and petioles densely rufous-pilose to -villous; wood simple; tendrils borne from leaf axils or peduncles, bifid. *Leaves* biternate, 5–13 cm long; petioles pu-

bescent throughout, ribbed on the upper surface; rachis winged, sometimes widest in the upper half; leaflets ovate to elliptic or obovate, rounded to acuminate at the apex, the acumen usually rounded and minutely apiculate, attenuate at the base, sparsely and deeply crenate in the distal ½–⅔, densely pubescent on the midrib and major veins above, sparsely pubescent on the surface, conspicuously pubescent throughout on the lower surface especially on the veins and with greatest concentration in the vein axils, the terminal leaflets 2.5–8.5 cm long, 1.3–4 cm wide; stipules inconspicuous, minute. *Inflorescences* generally axillary, often borne on the same short branches as the tendrils, the thyrses borne in a compacted, slender, spikelike structure to ca. 6 cm long; pedicels short or obsolete, elongating somewhat in fruit. *Flowers* 3.5–4.5 mm long; sepals densely tomentose, boat shaped and rounded at the apex; petals white, spatulate, rounded at the apex, ca. 3.5 mm long, weakly glandular within, the scales of the anterior petals ca. 2.5 mm long, villous, the crest ca. 0.7 mm long, longer than broad, shorter than the narrow, densely villous, deflexed appendage; staminate flowers with stamens to 2.8 mm long, the filaments densely villous; bisexual flowers not seen. *Fruits* suborbicular to broadly obovate, 13–20 mm long, rounded to emarginate at the apex, 3-locular, 3-winged, moderately to densely pilose, the medial crest sharply raised; seeds 1–3, globose, white-artillate at the base.

Variety *fuscescens* has frequently been confused with *Paullinia costaricensis* Radlk., and the two taxa cannot easily be distinguished vegetatively. *Paullinia costaricensis* can, however, be easily distinguished by the wingless fruit.

In Panama *P. fuscescens* flowers from December through March. Fruits mature principally in April and May.

Paullinia fuscescens var. *fuscescens* ranges from Mexico to Brazil and the West Indies. It generally occurs in dry areas. In Panama it occurs in tropical dry forest, premontane moist forest, and dryer parts of tropical moist forest.

Standley (1928) reports that this plant has been used in Panama as a treatment for poisonous insect bites. Duke (1968) reports that the seeds can be used as a fish poison. Common names for this taxon are "hierba de alacran" (Panama), "nistamal," "nistamalillo," "barbasco," "bejuco cuadrado," "cainpalaca," "bejuco costillon," "pico de guiloche," and "panoguera" (all Central America).

CANAL ZONE: Vic. Fort Sherman, *Croat 14156A* (MO). Chagres, *Fendler 43* (BM). E of Fort Clayton, *Harvey 5110* (F). Without exact locality, *Hayes 123* (NY). W side of Thatcher Ferry Bridge, *Lazor 2876* (SCZ). Amador Island, *Tyson 5407* (DUKE, SCZ). COCLÉ: Bismark, *Wall* (S). DARIÉN: Patiño, southern Darién, *Pittier 5705* (US). HERRERA: 1 m E of Chitre, *Croat 9696* (F, MO, PMA). LOS SANTOS: Beach at Monagre, *Burch et al. 1211* (GH, MO, US). 3 mi S of Las Palmas, *Croat 9724* (MO, NY, PMA, US, TEX). SE of Las Tablas, *D'Arcy 4226* (MO). Río Tonosí, vic. of Tonosí, *Lewis et al. 1539* (MO). Vic. of Tonosí, *Stern et al. 1868* (MICH, MO, US). 5 mi SE of Chitre, *Tyson et al. 3014* (MO, SCZ). Road from Tonosí to Guánico, *Tyson et al. 3120* (MO, SCZ). PANAMÁ: Along beach from Panamá Vieja to Bella Vista, *Allen 825* (F, MICH, MO, NY, P, U, US). 6 mi E of San Carlos, *Croat 14262* (MO). Taboga Island, *Hjerting & Rahn 608* (C, S). Vic. Panama City, *Macbride 2624* (F, US). Vic. Bella Vista, *Piper 5390* (US). Punta Paitilla, *Piper 5424* (F, US), *5433* (US). Taboga Island, *Standley 27854* (US). VERAGUAS: Trail between Cañazas and foot of Cordillera Central, headwaters of Río Cañazas, 300–600 m, *Allen 184* (MO). WITHOUT EXACT LOCALITY: *Seemann 597* (GH, NY). *Duchassaing s.n.* (P).

20b. **Paullinia fuscescens** var. **glabrata** Croat.[16] TYPE: Panama, *Croat 13235* (MO-2059597, holotype).

Tendrilled *lianas*; stems terete, inconspicuously pubescent and with many small lenticels; wood simple; tendrils borne from the leaf axils or peduncles, usually bifid. *Leaves* biternate, 5–12 cm long; petioles with a raised pubescent margin on the upper surface; rachis narrowly winged, the wing sometimes widest in the upper half; leaflets elliptic or oblanceolate, bluntly acute to acuminate, rarely rounded to emarginate at the apex, usually attenuate, sparsely crenate, glabrous above except on the sharply raised midrib, glabrate beneath except for tufts of trichomes in the vein axils, the terminal leaflets 3–9 cm long, 1–3.3(–5) cm wide; stipules minute, inconspicuous. *Inflorescences* terminal or axillary, often borne on the same short branches as the tendrils, to 10 cm long and 1 cm wide; pedicels short, 1.5–2.5 mm long at anthesis, puberulent, articulate about the middle or above. *Flowers* with a faint, sweet aroma, ca. 2.5–3.5 mm long; sepals sparsely to moderately appressed-pubescent, boat shaped, rounded at the apex; petals white; disc glands ovoid, present at the base of all four petals, yellow to orange, the scales of the anterior petals 1.5–1.7 mm long, the basal part about as broad as long, the deflexed appendage densely bearded, the scale crest slender, 0.7 mm long, often as long as the deflexed appendage; bisexual flowers with the stamens ca. 1.5 mm long, the ovary about as long as the stamens, the stigmas 0.7 mm long; staminate flowers with short stamens to 1.5 mm long, the longer ones to 2.5 mm long, the anthers narrowly ellipsoid, the pistil small, well concealed by the densely pubescent filaments, the stigmas 3, short. *Capsules* suborbicular to broadly obovate, to 2 cm long, red, sharply 3-angled, glabrate to sparsely pubescent, short-stipitate, beaked at the apex, the medial crest sharply raised, the wings 7–8 mm wide; seeds 1–3, oblong, shiny, black, the lower half enclosed in a white aril.

In Mexico var. *fuscescens* and var. *glabrata* merge to some extent and are difficult to separate with sterile material. In Panama the two varieties are clearly distinct on the basis of leaf shape, pubescence texture and size, and shape and degree of pubescence of flowers and fruits. In Mexico leaf shape and to some extent pubescence are not good characters for the separation of the two varieties.

Variety *glabrata* should not be confused with *Serjania pubescens* Seem. f. *glabrescens* Seem. This was considered a synonym of *Serjania fuscescens* by Radlkofer but actually is a synonym of *Paullinia costaricensis* Radlk.

Variety *glabrata* flowers principally in January and February with fruits developing to mature size by late February. Fruits mature mostly in April and May.

Paullinia fuscescens var. *glabrata* ranges from Mexico to Panama along the Caribbean coast. In Panama it appears to be restricted to wetter parts of tropical moist forest or in other life zones at higher elevations.

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[16] *Paullinia fuscescens* H.B.K. var. *glabrata* Croat, var. nov. Labrusca fruticosa; corpus lignosum simplex. Folia biternata; foliola elliptica aut oblanceolata, glabra superne praeter costam, glabrata infra praeter caespites in axillis venarum. Flores sepalis obscure adpressis-pubescentibus, manifeste pedicellati, minus quam 3 mm longi. Fructus suborbiculares, acute triangulata, glabrata ad sparsim pubescentes.

CANAL ZONE: Barro Colorado Island, *Croat 11278, 13235, 13809, 17053* (all MO), *14101* (FLAS, MO, SCZ). Vic. Fort Sherman, *Standley 30961* (US). Darién Station on Panama RR, *Standley 31622* (US). CHIRIQUÍ: Cerro Vaca, 900–1136 m, *Pittier 5374* (NY, US). VERAGUAS: Río Dos Bocas, 15.6 km NW of Santa Fe, *Croat 27725* (MO).

21. **Paullinia glomerulosa** Radlk., Monogr. Paull. 257. 1895. LECTOTYPE: Venezuela, *Warming 227* (C).—FIG. 7.

Tendrilled *lianas*; stems terete, glabrous; tendrils forked; wood simple. *Leaves* ternate-pinnate, 10–25 cm long, usually with 11(–15) leaflets (the lower set of pinnae biternate), glabrous except for the upper side of the petiole, rachis and midrib, as well as the lower midrib and major veins; petioles 1–6.5 cm long, margined or narrowly winged, margins wider upwards; leaflets lanceolate, acuminate, acute to attenuate at the base, subsessile, 1.5–10 cm long, 1–3 cm wide, ciliate, both surfaces often with granular punctations, entire or serrate-dentate in the upper half; stipules linear-lanceolate, to 1 cm long; foliage of young plants gray green. *Thyrses* aggregated, glomerate, less than 2 cm long, in leaf axils or on leafless stems, these often near the ground; pedicels ca. 4 mm long. *Flowers* white, ca. 3 mm long; sepals glabrous, orbicular to obovate and petaloid, to 3 mm long, spreading; petals narrowly obovate, ca. 3 mm long, sparsely granular-puberulent, the scales broader than the petals, ca. half as long, glabrous except for the villous margin, those of the anterior petals with simple orange crests, the deflexed appendage densely pubescent on the truncate lower margin only; anterior disc glands glabrous, ca. 1 mm long, ca. twice as long as broad; stamens with the filaments glabrous, somewhat flattened, united in the lower half; styles 3, short. *Capsules* suborbicular, sessile, glabrate, 1–1.5 cm long, reddish, with 3 narrow wings to 4 mm wide; seeds solitary, black, shiny, ca. 7 mm long, sparsely and softly pubescent with short trichomes, subtended by a white fleshy aril.

Paullinia glomerulosa can be confused with *P. serjaniaefolia*, *P. mallophylla*, and *P. funicularis*, but it is distinguished from the former by much more narrowly winged fruits and from the latter two species by sessile rather than stipitate fruits.

The species flowers in Panama during the rainy season from June through October. Fruits mature in the dry season mostly from January to March.

Paullinia glomerulosa is known from Mexico, Panama, Venezuela, and is infrequent in the West Indies. In Panama it is known from tropical moist forest and premontane wet forest.

BOCAS DEL TORO: Region of Almirante, *Cooper 212* (NY). CANAL ZONE: Barro Colorado Island, *Aviles 66* (F, MO); *Bangham 371* (A, F, US); *Croat 6179* (F, MO, NY, SCZ), *6224, 6377* (both MO, SCZ), *6466, 6701, 7265* (all MO), *7282* (F, MO, SCZ), *7997, 8102, 8724* (all MO); *Dwyer 1410* (MO, SCZ); *Ebinger s.n.* (MO); *Foster 1224* (DUKE, F, PMA), *1468* (DUKE, PMA); *Graham 208* (GH, MICH); *Hunnewell 16441* (GH); *Kenoyer 622* (US); *McDaniel 5018* (MO); *Shattuck 667* (F, MO); *Standley 40969* (US); *Weaver 1448* (PMA); *Weaver & Foster 1448* (DUKE); *Wetmore & Woodworth 852, 891* (both A, F), *917* (A); *Woodworth & Vestal 340* (A, MO). Near junction of Road C-2 and Gaillard Hwy., *Busey 353* (MO). Balboa, *Correll 12269* (GH). Thatcher Ferry Road, *Duke 5762* (GH, MO, PMA). Near Gatún RR Station, *Hayes s.n.* (US). Near Gatún, *Hayes 10* (GH,

US). Without exact locality, *Hayes 391* (K). Obisbo, *Standley 31720* (US). Río Indio, *Steyermark & Allen 17432* (G, MO, P). Farfan beach area, *Tyson & Blum 2611* (MO, SCZ). Maume and Gorgona, *Wagner s.n.* (M). DARIÉN: Río Cucunatí at Puente Quemado, *Duke 8817* (MO). San José River, *Duke & Bristan 398* (MO). Without exact locality, *Macbride 2708* (F, MO, US). Vic. La Palma, 0–50 m, *Pittier 5503* (F, M, NY, US). Vic. of Caná, 1750 ft, *Stern et al. 674* (G, GH, MO, US). Caná and vic., 2000–6500 ft, *Williams 951* (NY). PANAMÁ: Hills above Campana, *Allen 1868* (F, GH, MO, US). Cerro Campana, *McDaniel 6920* (MO). Around Alejuela, 30–100 m, *Pittier 2346* (GH, M, NY, US).

22. **Paullinia grandifolia** Benth. ex Radlk., Monogr. Paull. 227. 1895. TYPE: Brazil, Barra (Manaus), *Spruce 1537* (B, K, M).

Lianas; stems terete, finely and evenly lenticellate; wood simple. *Leaves* ternate-pinnate, 25–35 cm long, densely appressed-pubescent when young, soon glabrous, the lower pair of pinnae biternate; petioles 7.5–13 cm long, the petiole and rachis without wings but with an erect margin on the upper surface; stalk of the lower set of leaflets ca. 1 cm long; leaflets usually 11, lanceolate to oblong-elliptic, gradually long-acuminate, attenuate to acute at the base, (3–)5–14 cm long, (1.5–)2–4.7 cm wide, entire to remotely and inconspicuously crenate, drying grayish brown to reddish brown, the lateral veins slightly raised on both surfaces, the reticulate venation obscure; stipules narrowly triangular, acute, 6–8 mm long, densely tomentose outside, glabrous inside, soon deciduous. *Thyrses* solitary or in axillary panicles to 30 cm long; rachises granular-tomentose and hispid; smaller branches, pedicels, bracteoles, and calyces densely brownish-tomentose; bracteoles ovate-triangular, glabrous within, soon deciduous; pedicels to ca. 3 mm long. *Flowers* white; sepals 2.5–4.5 mm long, glabrous within; petals narrowly obovate, 5.5–6 mm long, the anterior scales ellipsoid, densely villous along the margins and over the surface of the deflexed appendage as well as on parts of the crest, the deflexed appendage densely bearded, the crest thick, shallowly bilobed, the lateral scales consisting merely of a fold, densely villous along its margin, the crest simple; disc glands 2, semicircular, glabrous, contiguous; stamens terete, weakly fused near the base; staminate flowers with the stamens to 4 mm long, the pistil reduced, 3-sided, glabrous except at the apex; bisexual flowers not seen. *Capsules* (in part after Radlkofer) subglobose, stipitate, abruptly contracted at the base, orange, ca. 1.7 cm long, glabrous and verrucose outside, glabrous inside, the pericarp ca. 2 mm thick, the stipe 5–6 mm long; seeds elliptic, arillate, the aril gray black, powdery (fide *Porter et al. 4129*).

The species is recognized by its terete stems, ternate-pinnate leaves, and elongated thyrses. Juvenile plants (*Croat 23019*) may have more conspicuously toothed leaves to 53 cm long with leaflets to 25 cm long and 7 cm wide.

In Panama flowering occurs during December and January. Mature fruits have been seen in late March when the plant had all new immature leaves. This indicates that the species may be deciduous.

Paullinia grandifolia ranges from Costa Rica (Limón Province) to Surinam, Brazil, and Peru. In Panama it is known from tropical wet forest.

COCLÉ: Vicinity of La Mesa, N of El Valle, ca. 1000 m, *Gentry 6821* (MO). DARIÉN: Cerro Tacarcuna, W Ridge, 1550–1700 m, *Gentry & Mori 14113* (MO). PANAMÁ: Cerro Azul, *Porter et al. 4129* (MO). VERAGUAS: 5 mi W of Santa Fe, *Croat 23003, 23019* (both MO).

23. **Paullinia kallunkii** Croat.[17] TYPE: Panama, *Mori, Kallunki & Hansen 4125* (MO-2248498, holotype; PMA, isotype).

Lianas; stems 3–6-costate when young, conspicuously hispidulous on the angles, becoming obscurely 3-angled or terete, glabrous; wood simple. *Leaves* ternate-pinnately compound, 16–20 cm long with 11 leaflets, the lowermost pair of segments biternate; petiole 2.5–5 cm long, without wings, hispidulous, both the upper and lower rachis winged, the medial ridge hispidulous, the broadest wings to 1 cm wide; leaflets oblong-lanceolate, acuminate at the apex, narrowly acute at the base, 1.7–10.5 cm long, 0.9–2.7 cm wide, entire, sometimes inconspicuously ciliolate, glabrous above except sometimes sparsely stiff-pubescent on the prominently raised, nearly square midrib, glabrous beneath except sometimes on the midrib, axillary tufts lacking, the major lateral veins numerous, often 20 or 30, inconspicuous, especially on the upper surface, scarcely more prominent than the reticulate venation, arising at almost 90° from the midrib, loop-connected near margin, the reticulate venation very close, prominulous on both surfaces; stipules linear-lanceolate, to ca. 1 cm long, prominently hirsute without and along the margin, glabrous within. *Inflorescences* axillary, the thyrses less than 1.5 cm long, glomerulate, the rachis weakly viscidulous, sparsely hispidulous; braceteoles narrowly triangular, 1–1.5 mm long, sparsely hispidulous; pedicels glabrate to hispidulous, 5–7 mm long in fruit, articulate below the middle. *Flowers* unknown; old sepals (persistent on fruits) glabrous except near the margin at the apex, to 2.5 mm long. *Fruits* round in outline, broadly 3-winged, red, subcordate at the apex, acute to attenuate at the base, briefly stipitate, 1.8–2.2 cm long, about as wide as long, 1?-locular, glabrous or sparsely puberulent near the base without, densely stiff, whitish-pubescent within; seed 1, ovoid to rounded, ca. 9 mm long, black, shiny, pubescent, enveloped at the base by a white aril.

Paullinia kallunkii is similar to *P. serjaniaefolia* but is distinguished from that species by its leaflets with prominulous reticulate venation, its numerous obscure lateral veins arising at about 90° to the midrib, its hispidulous stems, and its smaller fruits which are about as long as wide. It is named in honor of one of its collectors, Jackie Kallunki.

The type was collected in fruit in December. The species is known only from tropical wet forest in Panama.

DARIÉN: Headwaters of Río Tuquesa, ca. 2 km air distance from Continental Divide, *Croat 27109* (MO). PANAMÁ: El Llano-Cartí Road, 10.8 km from Interam. Hwy., 1100–1200 ft, *Mori et al. 4125* (MO, PMA). SAN BLAS: SE of Puerto Obaldía, *Croat 16812* (MO).

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[17] *Paullinia kallunkii* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex; rami juniores 3–6-costati, manifeste hispidi in angulis, rami maturi triangulati aut teretes, glabri. Folia ternato-pinnata, 11-juga; foliola retibus prominulis, nervis lateralibus numerosis obscuris sub angulo fere recto e nervo mediano abuentibus. Thyrsi axillares, glomerati. Fructus late trialatus, ruber, 1.8–2.2 cm longus et latus.

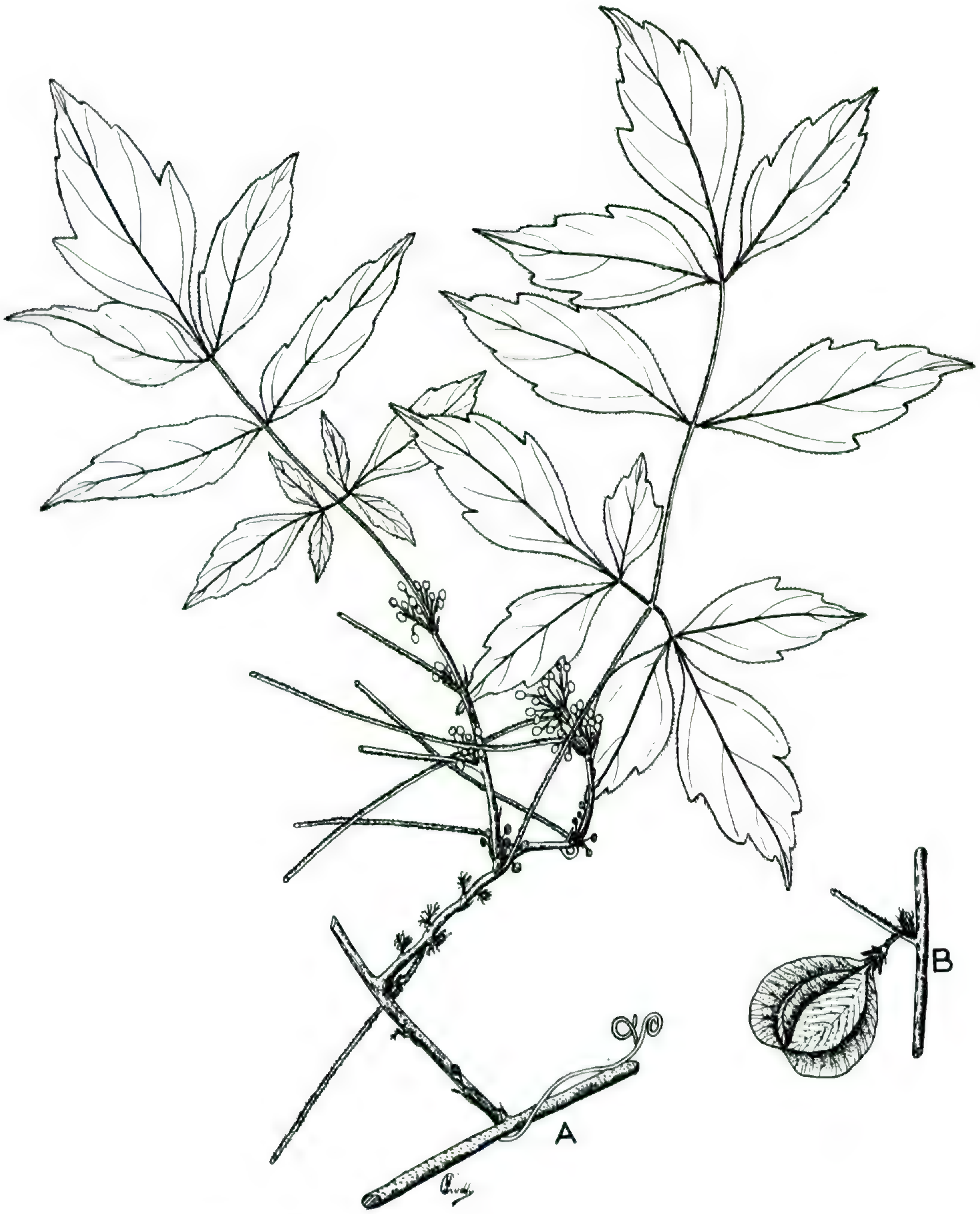

FIGURE 7. *Paullinia glomerulosa* Radlk.—A. Flowering branch (×3/5).—B. Fruit (×1 1/10). [After *Stern et al. 674* (MO).]

24. **Paullinia mallophylla** Radlk., Monogr. Paull. 188. 1895. TYPE: Costa Rica, ad Ujarus, *Oersted* (C, M).

P. verecunda Standley, Ann. Missouri Bot. Gard. 27: 316. 1940. TYPE: Panama, *Allen 1224* (MO).

Lianas; stems sharply 3–5-angled when young, viscidulous, puberulent to hispidulous on the angles, glabrate to puberulent elsewhere, terete to mostly

3-costate in age; wood composite or apparently simple (one or more of the three peripheral bundles small and difficult to see or possibly not developed). *Leaves* ternate-pinnately compound, 10–29 cm long, with 11 leaflets (2 sets above the ternate pair); petioles 0.8–10.5 cm long, without wings, narrowly canaliculate on the upper surface; lower rachis margined or narrowly winged, the upper rachis narrowly winged; petiole margins, petiolules, and medial ribs of rachises coarsely short-pubescent with stiff, acropetal or erect trichomes; leaflets oblong-lanceolate to oblong-elliptic or subrhombic, usually acuminate, sometimes bluntly acute at the apex, acute to attenuate at the base, 2–10 cm long, 1–5 cm wide, entire to remotely serrate-dentate, viscidulous, sparsely to densely short-appressed-pubescent on the larger veins beneath and on the midrib above, glandular-dotted, the axils of the lower veins not noticeably barbulate; stipules linear-lanceolate, 8–11 mm long, appressed-pubescent. *Inflorescences* axillary, the thyrses sessile, glomerate; rachises sparsely villous, shorter than the pedicels; bracteoles narrowly deltoid, hirsute; pedicels 4–7 mm long, hispidulous, articulate near the base. *Flowers* white; outer sepals hispidulous, to 2 mm long; petals oblong-obovate, 4–4.5 mm long, glabrous, the anterior scales elliptical, about half as long as petals, villous along the margin, the crest short, bilobed, orange, the deflexed appendage 2 or 3 times longer than the crest, densely villous marginally, scales of the lateral petals with the crest simple; disc glands 4, stiffly whitish-hirsute, the 2 anterior smaller, semicircular, the lateral oblong; stamens glabrous, the filaments compressed; bisexual flowers with the stamens 2.2–2.5 mm long, the pistil to 3.4 mm long, the ovary densely stiff white-pubescent throughout, the style ca. 2 mm long, sparsely puberulent to hispidulous, 3-branched in the upper third. *Capsules* red to brown, globose to broadly ellipsoid, truncate to broadly emarginate at the apex, rounded to obtuse at the base, narrowly stipitate, densely pubescent with stiffly erect grayish trichomes outside, white-villous inside, the body of the fruit 10–15 cm long, 3-winged, 3-celled, only one cell functional, the wing broadest toward the apex, the stipe 4–12 mm long; seed 1, globose to broadly ovoid, black, shiny, ca. 7 mm diam., sparsely pubescent, white-arillate at the base.

The species is distinguished by its ternate-pinnate leaves, sharply angled 3–5-costate young stems with composite wood, glomerulate inflorescences with pedicels longer than the rachises, and densely erect-pubescent, more or less globose, 3-winged fruits. It is most easily confused with *Paullinia funicularis* but may be distinguished from that species in having composite rather than simple wood and pedicels longer than the rachis. Radlkofer apparently relied entirely on the wood character for separation of the two species and as a result misidentified some collections cited in his monograph. The two species are perhaps most easily separated by pubescence of the leaves. Leaflets of *P. funicularis* have sparse long stiff trichomes on the midribs and also have a few similar trichomes over the upper surface. *Paullinia mallophylla* has a shorter, much denser, finer pubescence on the midribs and is glabrous on the upper surface between the veins.

In Panama *P. mallophylla* flowers from December through March, and fruits mature from March to May.

The species occurs in Costa Rica and Panama. In Panama it occurs from sea

level to 1,000 m in premontane wet forest, tropical wet forest, and premontane rain forest.

BOCAS DEL TORO: Vic. of Almirante, *Cooper 212* (F, NY, US). CANAL ZONE: 6½ km WNW of Gatún Dam, 165 m, *Nee 8952* (DUKE, GH, MO, P, PMA, RSA, US). CHIRIQUÍ: Quebrada Quanabanito beyond La Repressa W of Puerto Armuelles, *Croat 22059* (MO). Road from Paso de Canoas to Cañas Gordas, *Croat 22217* (MO). 2 mi SW Puerto Armuelles, *Liesner 333* (MO, PMA, TEX, US, VEN). Between Hato del Jobo and Cerro Vaco, 700–1000 m, *Pittier 5418* (NY, US). COCLÉ: Vic. of El Valle, *Allen 1224* (MO). El Valle, *Allen 4474* (G, MO). Cerro Pilón, 900–1173 m, *Liesner 771* (MO). COLÓN: Ca. 4 mi SW of Portobelo, *Croat 14109* (MO). Around Portobelo, 100 m, *Pittier 2436* (M, US). PANAMÁ: Cerro Campana, 2300 ft, *Blum & Miller 2286* (MO, SCZ); *Croat 14196, 14751, 17212* (all MO). Cerro Azul, *Croat 17320* (MO). Cerro Campana, *Dwyer et al. 4857* (MO, SCZ); *Porter et al. 4155, 4291* (both MO, SCZ). VERAGUAS: 5 mi W of Santa Fe, *Croat 23056* (MO).

25. **Paullinia morii** Croat.[18] TYPE: Panama, *Mori & Kallunki 4756* (MO-2249307, holotype; PMA, US, isotypes).

Lianas; stems terete, densely appressed-pubescent when young, conspicuously lenticellate and glabrous in age; wood simple. *Leaves* pinnately 7-foliolate, 11–25 cm long; petiole terete, 4.5–6.5 cm long, appressed-pubescent, narrowly canaliculate and puberulous on the upper surface; rachis terete, 3-ribbed on the upper surface; leaflets lanceolate, oblong-lanceolate to narrowly elliptic, gradually acuminate at the apex, attenuate to acute at the base, 6–12.5 cm long, 1.7–3.5 cm wide, entire, viscidulous, glabrous above except puberulent on the sharply raised midrib, glabrous beneath except for some sparsely barbulate vein axils, the reticulate venation prominently raised on both surfaces, especially beneath; petiolules 1–2 mm long, appressed pubescent or puberulent; stipules inconspicuous, soon deciduous. *Inflorescences* of solitary, unbranched thyrses 3–6 cm long, borne on leafless nodes in fruit; rachis, pedicel and outer sepals appressed-pubescent to puberulent; pedicels to 3 mm long in fruit, articulate about midway, the outer sepals pubescent inside, to ca. 2 mm long. *Flowers* unknown. *Fruits* obovate to ellipsoid, prominently stipitate, rounded to truncate or obtuse at the apex, 2–2.3 cm long, 1.5–2 cm wide, prominently 3-winged, red, the valves glabrous outside except on the style, the style persistent, ca. 1.3 mm long, 3-branched in the upper third, pulverulent-tomentose inside, the stipe 3–5 mm long; seeds shiny, black, glabrous.

Paullinia morii is distinguished by its pinnately 7-foliolate leaves with narrow, prominently veined leaflets and by its glabrous, 3-winged fruits which are mostly rounded at the apex. It is described in honor of its collector Scott Mori.

The species is known from a single collection made in Panama in a region bordering tropical wet forest and premontane rain forest. The collection made in February has full-sized but immature fruits.

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[18] *Paullinia morii* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex; rami teres. Folia 7-foliolato-pinnata; foliola lanceolata, oblongo-lanceolata ad anguste elliptica, 6–12.5 cm longa, 1.7–3.5 cm lata, retibus prominentibus. Thyrsi solitarii, 3–6 cm longi, sine ramis. Fructus obovatus ad ellipsoideus, manifeste stipitatus, rotundatus ad truncatum aut obtusus apicibus, manifeste trialatus.

VERAGUAS: NW of Santa Fe, 2.6 km from Escuela Agrícola Alto Piedra, ca. 700 m, *Mori & Kallunki 4756* (MO, PMA, US).

26. **Paullinia panamensis** Croat.[19] TYPE: Panama, *Duke 14319* (MO-2013318, holotype).

Lianas; stems deeply 3–6-sulcate or 3-sulcate with the costa weakly sulcate, conspicuously long-hispid, the trichomes reddish brown, to 6 cm long; texture of the surface smooth; wood simple. *Leaves* pinnately 7-foliolate, 22–45 cm long, sparsely but conspicuously hirsute on all surfaces and margins, viscidulous; petioles without wings, 3–16 cm long, prominently sulcate above; both lower and upper rachis broadly winged, the wings 6–10 mm wide; leaflets oblong-lanceolate to oblong-elliptic or oblong-oblanceolate, usually narrowly acuminate, sometimes acute at the apex, attenuate at the base on the terminal leaflet, inequilateral and acute to narrowly rounded on lateral leaflets at the base, 5–18 cm long, 1.5–6.7 cm wide, crenate mostly above the middle, the reticulate venation prominulous on both surfaces; stipules lanceolate-oblong, 14–20 mm long, several-nerved, glabrous except for the hispid margins. *Inflorescences* axillary, apparently solitary, short; rachis sparsely hispid; bracteoles narrowly deltoid, glabrous, thickened greatly at the base, especially medially; pedicels to 2.5 mm long, glabrous, articulate about midway. *Flowers* white; sepals rounded, glabrous; petals obovate, glabrous, glandular within, the anterior scales with crests emarginate, the deflexed appendage ciliate; disc glands 2, semicircular, glabrous; stamens with the filaments glabrous; ovary glandular. *Fruit* not known.

Paullinia panamensis is distinguished by its conspicuously hispid, 7-foliolate leaves. It has been confused with *P. hispida* Jacq. but that species has bipinnate or ternate pinnate leaves with 4–6 sets of leaflets.

With so little material of the species available, its phenology is uncertain but it probably flowers in the rainy season. The type has immature inflorescences in September.

The species is known only from eastern Panama in tropical moist forest.

PANAMÁ: Piriá—Cañasas Trail, ca. 100 m, *Duke 14319* (MO). SAN BLAS: E of Puerto Obaldía, *Croat 16942* (MO).

27. **Paullinia pilonensis** Croat.[20] TYPE: Panama, *Dwyer & Lallathin 8971* (MO-2195310, holotype).

Lianas; stems terete, glabrous to sparsely short-puberulent; wood simple. *Leaves* pinnately 5-foliolate, drying dark; petiole ca. 2.5 cm long, terete, narrowly canaliculate on the upper surface near the apex; rachis canaliculate, without

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[19] *Paullinia panamensis* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex; rami 3–6-sulcati, manifeste longi-hispidi. Folia 7-foliolato-pinnata, sparsim sed manifeste hirsuta omnino. Thyrsi axillares, solitarii, breves. Fructus ignotus.

[20] *Paullinia pilonensis* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex; rami teres. Folia 5-foliolata-pinnata; petiolus rhachisque nuda, minute puberula. Inflorescentia axillaris, sine ramis, 15–20 cm longa. Fructus globosus, sessilis, ad 2.5 cm diametrum, 6-sulcatus, interius sparsim villosus.

wings; petiole and rachis minutely puberulent; leaflets narrowly ovate to ovate-elliptic, acuminate at the apex, the acumen blunt, attenuate to rounded at the base, 2–7 cm long, 1.5–3 cm wide, entire to remotely serrate, glabrous or nearly so, the midrib scarcely raised on the upper surface, the reticulate venation somewhat prominulous on both surfaces; stipules small, soon deciduous. *Inflorescences* axillary, unbranched, 15–20 cm long; peduncle 4–8 cm long puberulent to scabridulous. *Flowers* not known; sepals sometimes persisting on fruit, the outer sepals almost semicircular, densely strigose without, glabrous within. *Fruits* subglobose, shortly stipitate, to 2.5 cm diam., prominently and equidistantly 6-sulcate, mammillate at the apex, moderately hispidulous outside, becoming glabrous, sparsely villous inside, the surface easily visible, shiny; seeds 1 or 2, ellipsoid, ca. 1.5 cm long, covered throughout with a pithy mesocarp, basal aril lacking.

*Paullinia pilonens*is is most easily confused with *P. costata* Schlecht. & Cham. but differs from that species in having globose, 6-sulcate fruits only sparsely villous within. *Paullinia costata* has 3-costate fruits that are stipitate and gradually taper to the base.

Paullinia pilonensis is known only from the type collection which had fruits during late July in a region of premontane rain forest in Panama.

COCLÉ: Cerro Pilón, 3100 ft, *Dwyer & Lallathin 8971* (MO).

28. **Paullinia pinnata** L., Sp. Pl. 366. 1753. TYPE: not seen.

P. hostmanni Steud., Flora 27: 725. 1844. TYPE: Surinam, *Hostmann & Kappler 1211* (BM, S).

P. pendulifolia Rusby, Mem. New York Bot. Gard. 7: 291. 1927. TYPE: Bolivia, Pampas near Lake Rogagua, *Rusby 1622* (NY).

Lianas; older stems 3-ribbed, the younger ones mostly 6-ribbed, glabrous to puberulous; wood composite; tendrils forked. *Leaves* pinnately 5-foliolate, strigillose on the upper side of the petiole, rachis, and midrib; petiole to 8 cm long; petiole and rachis winged, their margins ciliate; leaflets elliptic, short-acuminate, obtuse at the base, 5–11 cm long, 2.5–4.5 cm wide, with granular punctations throughout on both surfaces and with tufted vein axils beneath, conspicuously crenate throughout most of the margin, the teeth glandular; stipules lanceolate, densely appressed-pubescent, less than 10 mm long, deciduous. *Thyrses* solitary, 5–25 cm long, axillary or borne at forks of tendrils, spikelike. *Flowers* white or yellowish, ca. 3 mm wide, wider than long; bracteoles linear-lanceolate, 2.5–4.5 mm long, appressed-pubescent on both surfaces; sepals equal, 5, appressed-pubescent; petals narrowly obovate, 2.5–3 mm long, the anterior scales obovate, fused about half their length to the petal, villous, the deflexed appendage and its villous margin extending more than halfway to the base of the scale, the crest obovate, orange; staminate flowers with the stamens exserted, ca. 2.5–3 mm long, filaments flattened, villous, the pistil short, 3-sided, villous at the apex, the styles glabrous, equalling the ovary; bisexual flowers with the stamens to 2.5 mm long, the ovary ovoid, densely appressed-pubescent to nearly glabrous, the ovary and style together ca. 4 mm long, the style about as long as the ovary, glabrous, 3-branched in the upper third. *Capsules* broadly clavate, 2–4

cm long, rounded to truncate and abruptly acuminate at the apex, gradually tapered to a long-stipitate base, red, 3-celled, round to bluntly 3-sided in cross-section; seeds 1–3, ellipsoid, 1.5–3 cm long, black, shiny, partly enclosed by a white aril.

The species is distinguished by its 5-foliolate leaves with winged rachises, winged petioles, barbulate vein axils, and elongate inflorescences. In Panama it is most easily confused with *Paullinia sessiliflora* var. *angustirachis* which, though morphologically similar, is ecologically distinct. See that species for a discussion of the differences. It may also be confused vegetatively with *P. alata* which is similarly pubescent, but that species has glomerate-fasciculate inflorescences.

In Panama flowering occurs principally in the rainy season between June and November with fruits maturing mostly from September to January. Flowering also occurs rarely in the dry season.

Paullinia pinnata is a variable species ranging throughout tropical America, and it is also known from tropical Africa. In Panama it is known from tropical moist forest and premontane wet forest.

The seeds of *P. pinnata* are used as a fish poison while the stems are used as cordage. According to Duke (1968) the roots are chewed by the Indians of Darién for coughs. Common names reported include "barbasco" (Panama), "apgi" (Cuna).

BOCAS DEL TORO: Water Valley, *von Wedel 883* (GH, MO). Vic. of Chiriquí Lagoon, *von Wedel 1154* (GH, MO, US), *1518* (GH, MO). CANAL ZONE: Barro Colorado Island, *Aviles 989* (F); *Bailey & Bailey 310* (GH); *Croat 11111* (MO), *12845* (MO, NY, SCZ); *Foster 1059* (DUKE, PMA); *Kenoyer 424* (US); *Shattuck 989* (MO, US); *Wetmore & Woodworth 879* (A). Gaillard Hwy. at Río Coco Solo, *Croat 14170* (MO). Chagres, *Fendler 455* (MO). Coco Solo, *Gentry 6282, 6493, 6498* (all MO), *6793* (DUKE, MO, PMA). 2 mi N of Gatún Locks, *Lazor & Blum 5428* (MO). Margarita swamp S of France Field, *Maxon & Valentine 7037* (US). Along Río Trinidad, near sea level, *Pittier 4035* (NY, US). Near Fort Randolph, *Standley 28624* (US). PANAMÁ: Cerro Azul, *Duke 9361* (MO). SAN BLAS: Just N of Mandinga airport, *Duke 14850, 14851* (MO).

29. **Paullinia pterocarpa** Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 356. 1862. TYPE: Colombia, Llano San Martín, *Triana 5599* (Herb. Planchon, ?MPU, not seen).

P. triptera Triana & Planch., Ann. Sci. Nat., sér. 4, 18: 356. 1862. TYPE: Colombia, *Goudot* (P).
P. excisa Radlk., Monogr. Paull. 273. 1895. TYPE: Tobago, *Eggers 5723* (A, US).
P. trisulca Radlk., Bull. Herb. Boiss., sér. 2, 5: 323. 1905. TYPE: Costa Rica, buissons á las Vueltas, Tucurrigue, 635 m, *Tonduz 12902* (B, destroyed, MO, photo).
P. mexiae Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 155. 1940. TYPE: Ecuador, Napo-Pastaza, near Tena, 400 m, *Mexia 7144* (F).
P. vaupesana Killip & Cuatr., Revista Acad. Colomb. Ci. Exacta 4: 344. 1941. TYPE: Colombia, *Cuatrecasas 7110* (US).

Lianas; stems glabrous, terete or 3-ribbed when young, usually markedly 3-ribbed in age; wood simple. *Leaves* pinnately 5-foliolate, glabrous; petioles without wings, ribbed above, (2.5–)5–9(–11) cm long, to 14 cm on juveniles; rachis without wings; leaflets ovate to elliptic to ovate-elliptic, long-acuminate or rarely acute at the apex, the terminal leaflets attenuate, to obtuse or rounded at

the base, entire to remotely coarse-crenate, (4–)6–17(–23) cm long, (2.2–)3.5–8 (–9) cm wide, glandular-punctate, the reticulate venation prominulous on both surfaces; stipules lanceolate-linear, 8–12 mm long, striate, usually glabrate. *Inflorescences* usually solitary thyrses 1–6.5 cm long, borne in the leaf axils, at leafless nodes, or on tendrils, sometimes glomerulate with up to 4 thyrses at a node; rachis and pedicels puberulous to glabrate; bracteoles ovate-deltoid, puberulous to glabrate, ciliate; pedicels articulate below the middle, 6–10 mm long in fruit. *Flowers* white, ca. 4 mm long; sepals 5, glabrous or puberulent, irregular, ciliate; petals obovate, to ca. 3 mm long, often asymmetrical, the anterior scales ca. 2 mm long, ciliolate, about as broad as long, the inner margins extending laterally and overlapping, the crest small, emarginate, the deflexed appendage longer than the crest, glabrous except the long-ciliolate margin, the cilia about twice as long as the appendage itself; disc glands semicircular, hispidulous throughout, lacking at the base of the lateral petals; stamens with filaments flattened, glabrous; ovary pubescent near the apex; staminate flowers with 3 sessile stigmas; bisexual flowers with the style 3-branched at the middle. *Capsules* broadly obovate, rarely elliptic, emarginate to almost truncate at the apex, red, conspicuously 3-winged, 3-celled, only 1 cell functional, 2–4 cm long, glabrous, the wings 3–7 (–13) mm diam., broadest toward the apex, the valves striate outside, tomentose inside, the body 2–3.4 cm long, 1.5–2.5 cm wide, the stipe 2–7 mm long; seed 1, ca. 9 mm long, ovoid to ellipsoid, black, sparsely pubescent, the lower half white-arillate.

Paullinia pterocarpa is most similar to *P. allenii* but is distinguished from that species by its slender, persistent, more or less glabrous stipules, shorter inflorescences, and smaller flowers. More flowering collections may show greater similarities between these two closely related taxa. *Gentry & Dwyer 3632* (MO) has fruits unusually large for this species, measuring to 4 cm long, with the wing to 1.3 mm wide. Possibly it is a distinct species. The species is closely related to and perhaps inseparable from *P. caloptera* Radlk. from Brazil.

Radlkofer (1933–1934) reported *P. subnuda* for Panama. I have seen the Haenke collection from Prague which he cited and it is *P. pterocarpa*.

Flowers are known for certain only from August and September. Fruiting collections have been made mostly from July to October but also once in February.

The species ranges from Costa Rica to Peru though Peruvian material differs in being pubescent on the stems and veins of the leaflets. In Panama the species occurs from sea level to 800 m, principally in premontane wet forest and tropical wet forest, but also in wetter parts of tropical moist forest.

BOCAS DEL TORO: Without exact locality *von Wedel 337* (GH, MO). Water Valley, *von Wedel 596* (GH, MO, U), *904* (GH, MO, US). Vic. of Chiriquí Lagoon, *von Wedel 1152* (GH, MO, US), *1209* (GH, MO), *1385* (GH, MO, US), *2762* (GH, MO, NY, US), *2770* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 46* (F); *Croat 14850* (MO, SCZ). Coco Solo, *Gentry 6490* (MICH, MO, PMA, US). Pipeline Road ca. 6 mi N of Gamboa, *Tyson 6662* (MO). CHIRIQUÍ: 12 mi W of Puerto Armuelles, 400–500 m, *Liesner 198* (CAS, DUKE, F, GH, MO, NY, PMA, US). COCLÉ: La Mesa, above El Valle, 800 m, *Croat 25373* (MO, NY, PMA, RSA, US). 4 mi from El Valle, *Gentry & Dwyer 3632* (MO, PMA, US). 5 mi NW of El Valle de Antón, *Luteyn 1225* (DUKE). 2–4 mi N of Interam. Hwy., *Luteyn 4124*

(DUKE). COLÓN: Río Guanche, *Gentry 6321* (DUKE, GH, MO, PMA, US). PANAMÁ: 3 mi NE of Altos de Pacora, 500–800 m, *Croat 22760* (MO). On trail to Cerro Campana, *Kirkbride & Hayden 275* (MO, NY, SCZ). El Llano-Cartí Road at km 8–11, 300–400 m, *Mori 7753* (CAS, MO, PMA). Along Cartí Road, beyond Chepo, *Wilbur & Luteyn 19486* (DUKE).

30. **Paullinia rugosa** Benth. ex Radlk., Monogr. Serj. 75. 1875. TYPE: Brazil, Amazonas, Manaus, *Spruce 1206* (K, NY).—FIG. 8.

P. subcordata Benth. ex Radlk., Monogr. Serj. 75. 1875. TYPE: Brazil, Barra, Manaus, *Spruce 1184* (F, K, NY, P).
P. fimbriata Radlk., Bull. Herb. Boissier, sér. 2, 5: 322. 1905. TYPE: Costa Rica, bords d'une riviere au-dessus de Tsaki, Talamanca, 400 m, *Tonduz 9414* (US).
P. ovalis Radlk., Bot. Jahrb. Syst. 54, Beibl. 117: 43. 1916. TYPE: Colombia, near Orocue at Río Meta, 100–400 m, *Lehmann 8781* (not seen).
P. colombiana Cuatr., Revista Acad. Colomb. Ci. Nat. Exacta 8: 478. 1952. TYPE: Colombia, State of Boyaca, *Lawrence 516* (F).

Tendrilled *lianas*; stems (3–)5-ribbed, obscurely so in age and ca. 2–2.5 cm diam.; sap milky; stems, tendrils, petioles and rachises densely reddish brown hirtellous-tomentose; tendrils stout, forked; wood simple. *Leaves* pinnately 5-foliolate, 20–40(–60) cm long, the leaflets opposite; petioles 5–18(–30) cm long, terete; leaflets broadly elliptic to ovate or obovate, acuminate, attenuate to rounded and sometimes inequilateral at the base, 12–25(–35) cm long, 7–13 (–17) cm wide, hirtellous above on the veins, hirsute throughout beneath, especially on the veins, the lateral veins ending in apiculate teeth, the reticulate veins prominulous; stipules semiorbicular, sericeous, 1–2 cm diam., with fimbriate margins. *Thyrses* short, closely congested on slender, bracteate, spikelike inflorescences, these simple and borne in leaf axils or on tendrils, or compound and terminal. *Flowers* white, ca. 3.5 mm long; sepals tomentulose, orbicular or ovate and short-acute; petals obovate, ca. 3 mm long, the scales ca. 2.5 mm long, with the lateral margin weakly ciliate, the deflexed appendage villous-bearded, truncate, the crest orange, weakly lobed; disc glands about as broad as long, sparsely pubescent, weakly concave on the outside; filaments densely wooly throughout, the pubescence partly covering the base of the anthers; ovary and outer surface of styles densely pubescent. *Capsules* bright red orange, suborbicular, to 1.5 cm diam., weakly beaked, stipitate, round in cross-section, densely tomentose, the stipe 3–4 mm long; seed solitary, subglobular, ca. 1 cm diam., black, covered by a thin white aril.

The species is distinguished by its large, densely rufous-pubescent leaves and stems and by its large, semiorbicular, fimbriate stipules.

Paullinia rugosa flowers from July to September but mostly in August in Panama. Fruits mature mostly in September.

The species ranges from Costa Rica to Peru and Brazil. In Panama it is known from tropical moist forest and premontane wet forest.

CANAL ZONE: Barro Colorado Island, *Aviles 958* (F, US); *Bangham 446* (F, US); *Croat 6036* (MO, SCZ), *6381* (DUKE, F, MO, NY, SCZ), *10326* (MO), *11783* (MO, SCZ), *14009* (MO); *Foster 1297* (DUKE); *Salvosa 908* (A); *Wetmore & Woodworth 25* (F). Fort San Lorenzo, *Allen 5136* (MO). Pipeline Road, *Correa & Dressler 306* (SCZ). Road S-10, N of Escobal, *Croat 12435* (DUKE, F, MO, NY). Coco Solo ATTC, *Dwyer & Duke 7889* (DUKE, MO). Pipeline Road, *Gentry 1901* (MO, SCZ). Coco Solo, *Gentry 6084* (MO). ½ mi N

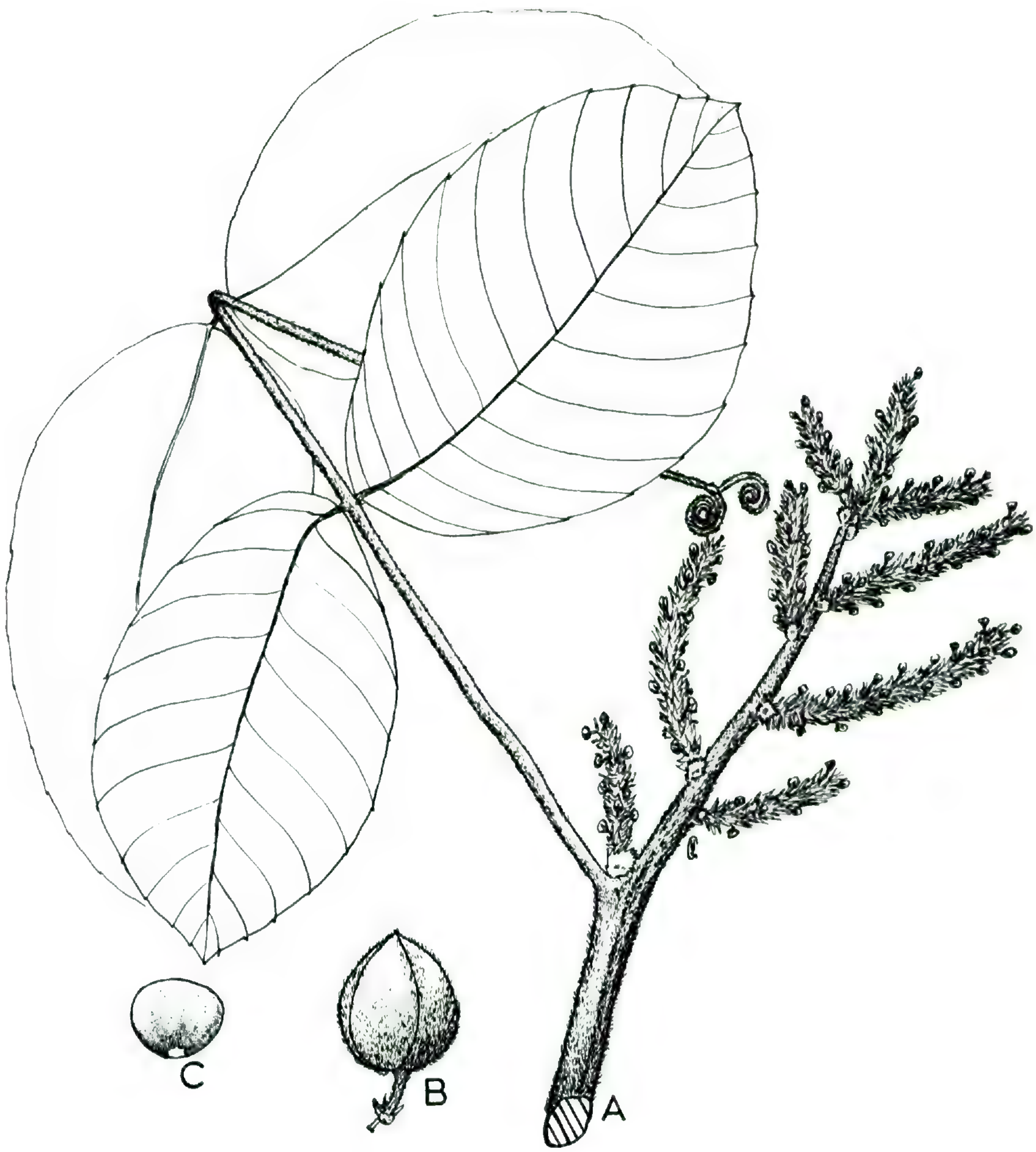

FIGURE 8. *Paullinia rugosa* Benth. ex Radlk.—A. Flowering branch (×3/10).—B. Fruit (×1⅕).—C. Seed (×1⅕). [After *Allen 5136* (MO).]

of Gamboa, *Lazor & Tyson 5666* (MO). 12–20 mi NW of Gamboa, 0–100 m, *Mori & Kallunki 1732* (MO). 4 km NW of Gamboa, 50 m, *Nee 7083* (COL, F, GH, K, MEX, MICH, MO, NY, P, PMA, US). 1 km N of Gamboa, 200–220 m, *Nee 7435* (MO). COLÓN: María Chiquita, *Dwyer & Kirkbride 7789* (DUKE, MO). Loma de la Gloria, near Fato, *Pittier 4427* (US). PANAMÁ: Cerro Jefe, *Croat 17358* (MO). El Llano-Cartí Road, 12 mi above Pan-Am. Hwy., 200–500 m, *Croat 22861* (MO). SAN BLAS: Mainland opposite Playa Chico, *Gentry 64111* (MO). VERAGUAS: 11 km beyond Santa Fe, 650 m, *Croat 25653* (MO). Between Escuela Agrícola Alto Piedra and Río Dos Bocas, 5–8 km from the school, 730–770 m, *Croat 25950* (MO). WITHOUT EXACT LOCALITY: *Hayes 574* (NY).

31. **Paullinia serjaniaefolia** Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 8: 356. 1862. TYPE: Colombia, *Karsten* (W, not seen, MO, photo).

P. venusta Radlk., Bull. Herb. Boissier, sér. 2, 5: 324. 1905. TYPE: Costa Rica, *Pittier 7664* (BR).

Lianas; stems variable, 3–5-sided when young, viscidulous, glandular, glabrous or sparsely pubescent with occasional long trichomes, soon terete or 3-sulcate; wood simple or rarely with one costa apparently forming a separate bundle. *Leaves* variable, 8–30 cm long, bipinnately compound, ternate-pinnate with 11 leaflets or with the lowermost segments sometimes 5-foliolate; petioles 1–10 cm long, without wings or rarely narrowly winged near the apex, marginally ribbed on the upper surface; lowermost rachis margined or narrowly winged, the other rachises narrowly winged, rarely only margined, the wings broadest toward the apex; leaflets lanceolate-elliptic, oblong-elliptic to subrhombic, acuminate at the apex, attenuate to acute at the base, (1.5–)3–14 cm long, (1–)1.5–5 cm wide, entire to crenate-dentate in the outer ½–¾, the upper surface glabrous except sometimes sparsely pubescent on the midrib, glabrous beneath except usually densely barbulate in the vein axils, sometimes sparsely pubescent on the midrib; stipules linear-lanceolate, 7–15 mm long, sparsely appressed-pubescent. *Inflorescences* axillary or more commonly borne at leafless nodes well below leaves, sometimes borne at ground level, rarely on tendrils; thyrses less than 2 cm long, in short-branched, glomerate clusters; pedicels 4–6 mm long, longer than the rachis, glabrous or sparsely appressed-puberulent, articulate near the apex. *Flowers* white, nearly glabrous, the outer sepals oval to obovate, ciliate; petals obovate, to 3.5 mm long, glandular on both surfaces, the anterior scales ⅔ as long as the petals, obovate-elliptic, prominently ciliate; crest 0.5 mm long, obovate, orange, the deflexed appendage equalling the crest, densely bearded in the lower ¼ and along the lateral margins; disc glands oblong, sparsely puberulent on both sides; filaments flattened, densely villous throughout; bisexual flowers with the stamens 2 mm long, the pistil to 3.5 mm long, the ovary less than 1 mm long, trigonous, densely hispidulous, the style glabrous, 3-branched in the upper ¼. *Fruits* broadly 3-winged, round or nearly so, cordate at the apex, truncate to rounded or cordate at the base, 2–3 cm long, 2.5–3.3 cm wide, red, glabrous or nearly so outside, densely erect-pubescent inside, the nerves prominulous, the wings to ca. 1 cm wide; seed 1, globose to ellipsoid, black, shiny, densely soft-pubescent, white-arillate at the base.

The species may be confused with either *Paullinia mallophylla* or *P. funicularis* which are also ternate-pinnately compound. See the key for ways to distinguish them. *Paullinia serjaniaefolia* is one of the most variable species of Sapindaceae, and the material as treated may involve another species. However, despite considerable variation in compounding of leaves, stem anatomy, disposition of the inflorescences, phenology, and ecology, no consistent characters allow separation of the material into more taxa.

In Panama flowering occurs to some extent throughout the year. Flowering

collections have been made in January, March, May, July, August, and December. Fruiting collections have similarly been made throughout the year.

Paullinia serjaniaefolia ranges from Costa Rica to Colombia. In Panama it occurs principally in premontane wet forest and tropical wet forest but also in premontane moist forest and tropical moist forest.

CANAL ZONE: Farfan Beach, *Gentry & Dwyer 3552* (NY). CHIRIQUÍ: 8 mi W of Puerto Armuelles, 200 m, *Liesner 359* (MO). COCLÉ: La Mesa, 650–710 m, *Mori & Kallunki 1899* (MO). COLÓN: Vic. of Río Piedras on road to Portobelo, *Blum et al. 2512* (MO, SCZ). Santa Rita Ridge, *Croat 13192* (MO). Río Guanche, *Foster & Vocelka 2197* (DUKE, MICH, MO); *Gentry 8809* (MO, PMA); *Kennedy & Foster 2189* (MO). Santa Rita Ridge Road, *Mori & Kallunki 2096, 3050* (both MO). Río Guanche, 20 m, *Mori & Witherspoon 7947* (CAS, MO, PMA); 5–30 m, *Nee 7126* (CAS, DUKE, GH, K, MO, P, PMA, VEN). DARIÉN: Río Yape, *Bristan 1419* (MO). 1–5 mi downstream from El Real, *Duke 4932* (DUKE, MO, SCZ). Loma Cuasí, behind Manené, *Duke 13603* (MO). Río Mortí, drill site 7, 250 m, *Duke 14203* (NY). Cerro Tacarcuna, S slope, 1250–1450 m, *Gentry & Mori 13935* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1539* (MO). Caná-Cuasí Trail, camp 2, Chepigama District, 2000 ft, *Terry & Terry 1485* (US). PANAMÁ: Cerro Jefe, *Croat 14448* (MO); *Dwyer & Gentry 10256* (MO). Campo Tres, 500–800 m, *Croat 22703* (MO). El Llano-Cartí-Tupile Road, *Kennedy et al. 2438, 3144* (both MO); *Liesner 1170* (MO); *Luteyn & Wilbur 4660* (DUKE). SAN BLAS: SE of Puerto Obaldía, *Croat 16777* (MO). Above Puerto Obaldía, *Gentry 1505* (MO, SCZ). VERAGUAS: 3.9–5 mi N of Santa Fe, 500–1000 m, *Gentry 3005* (F, MO, U). Río Primero Brazo, 5 mi NW of Santa Fe, *Liesner 802* (MO, SCZ).

32. **Paullinia sessiliflora** Radlk., Contr. U.S. Natl. Herb. 1: 317. 1895.

32a. **Paullinia sessiliflora** var. **angustirachis** Croat.[21] TYPE: Panama, *Croat 14501* (MO-2045731, holotype).

Lianas; younger stems 3–6-costate, at least sometimes becoming terete in age, scurfy and hirtellous to puberulent; wood simple. *Leaves* pinnately 5-foliolate; petiole 7–14 cm long; petiole and rachis winged, glabrous to strigillose or puberulent, the rachis wing 3–8 mm wide, slightly wider than the wing of the petiole; leaflets narrowly elliptic, lanceolate-elliptic or ovate-elliptic, gradually acuminate, inequilateral and acute to narrowly obtuse at the base, 7–19 cm long, 1.5–7 cm wide, entire or crenate mostly in the outer half, the teeth often glandular, the upper surface nearly glabrous or puberulent on the midrib, the lower surface glabrous except hirtellous to puberulent on the midrib and often with barbulate vein axils; stipules linear-lanceolate, appressed-pubescent, 1–3 cm long. *Thyrses* solitary, to 20 cm long, moderately stout, to 3 mm diam., densely tomentose throughout, the bracteoles narrowly ovate-triangular, 2–4 mm long, densely grayish appressed-pubescent outside, glabrous inside. *Flowers* to 5 mm long and 5 mm wide, sessile or with pedicels 1 mm long; sepals 2.5–4 mm long, the outer smaller,

[21] *Paullinia sessiliflora* Radlk. var. *angustirachis* Croat, var. nov. Labrusca fruticosa; corpus lignosum simplex; rami juniores 3–6-costati; rami maturi teres. Folia 5-foliata-pinnata; petiolus rhachisque alata; foliola anguste elliptica, lanceolata-elliptica aut ovata-elliptica, 7–19 cm longa, 1.5–7 cm lata, integra aut crenata in dimidio exteriore, dentibus glandulosis, fere glabra praeter costas, saepe axillaris venarum caespitosis; stipulae lineares-lanceolatae, 1–3 cm longae. Thyrsi solitarii, ad 20 cm longi, ad 3 mm diametro; bracteolae anguste ovatae-triangulae, 2–4 cm longae. Flores ad 5 mm longi et 5 mm lati. Fructus anguste obovatus, 2–3.5 cm longus, stipitatus. Florescentia tempu pluviali.

ovate-oblong, pubescent on both surfaces, the inner oblong, pubescent on the outer surface; petals oblong-obovate, to 5 mm long, the scales ⅔ as long as petals, fused to the lower ¼ of the petal, sparsely villous to silky long-pubescent along the margins, the anterior pair elliptic with deflexed appendages about as broad as long, glabrous except for a densely pubescent fringe, the fringe equalling the appendage, the crest orange, obovate, thin, the scales of the lateral petal consisting of an elongated fold, the crest present but reduced; disc pubescent, the anterior glands obovate or obcordate, ca. 0.5 mm long, glabrous, the lateral disc glands reduced or obsolete; filaments flattened, villous; staminate flowers with the stamens to 3.5 mm long, the pistil very reduced, more or less glabrous; bisexual flowers with the stamens 2.5–3 mm long, the ovary ovoid, densely sericeous, ca. 2 mm long, the style 1.5 mm long, 3-branched in upper ⅓–½. *Capsules* narrowly obovoid, 2–3.5 cm long, stipitate, acute or rarely truncate to rounded at the apex with an acute or mammillate projection, 3-locular, red at maturity, finely longitudinally striate, sparsely short-pubescent, the stipe thick and short to long and slender; seeds usually 2, sometimes 3, black, drying dark brown, shiny, ca. 1 cm long, enveloped on most of both sides with a thin white aril.

Paullinia sessiliflora var. *angustirachis* is easily confused with *P. pinnata* but is distinguished by stems with simple wood, longer stipules, leaflets that are often entire and longer in relation to their width (Panama), and vein axils that are less conspicuously barbulate. This taxon flowers in the dry season while *P. pinnata* flowers in the rainy season. Vegetatively the species is confused with *P. alata* which also has 5-foliolate leaves.

Paullinia sessiliflora var. *angustirachis* differs from the typical variety which ranges from Mexico to Nicaragua in having longer and narrower leaf rachises and narrower, usually less toothed leaflets. *Paullinia sessiliflora* var. *angustirachis* flowers in January and February. Fruits may be fully formed by February and mature from May to September, especially in June and July.

Paullinia sessiliflora var. *angustirachis* is known only from Panama, principally from tropical moist forest on the Pacific slope, but it has also been found in tropical moist forest at Puerto Obaldía, San Blas Province. A sterile collection (*Croat 27118*), possibly this species, has been collected in premontane wet or tropical wet forest in Darién Province.

CHIRIQUÍ: 6 mi S of Puerto Armuelles, 0–150 m, *Liesner 485* (MO). DARIÉN: Headwaters of Río Chico, *Allen 4600* (MO). Road to Pinogana near El Real, *Croat & Porter 15470* (MO). Road from El Real to Pinogana, *Duke 5005* (MO, SCZ). Río Chico across from Boca de Tesca, *Duke 5213* (GH, MO). Agua Fría, ca. 8 mi N of Santa Fe, *Duke 10102* (MO). Ca. 2 mi N of Santa Fe, *Duke 10229, 10713* (both MO). 1–4 mi N of Pucro, *Duke 13052* (MO). Río Pirre, *Kennedy 2887* (MO). Trail between Río Escucha Ruido and Río Tuira, *Stern et al. 574* (MO, US). Marragantí and vic., 100–400 ft, *Williams 1014* (NY). PANAMÁ: 1 mi E of El Llano, *Croat 14496, 14501* (both MO). Dam site on Bayano River, S of Cañita, *Croat 14510* (US), *14519* (MO). Piriá-Cañazas trial near Piriá, 100 m, *Duke 14344* (MO). Río Pasiga, *Gentry 2306* (MO). Trail from Río Espave toward Río Agua Clara, *Gentry 3766* (F, MO, U). 10–15 km from Bayano crossing on trail to Santa Fe, *Gentry 3827* (MO, U). SAN BLAS: Puerto Obaldía, *Croat 16744a* (MO). E of Puerto Obaldía, *Croat 16925* (MO).

33. **Paullinia sternii** Croat.[22] TYPE: Panama, *Stern et al. 574* (MO-1758530, holotype; GH, US, isotypes).

Lianas; stems 3–6-sulcate, sparsely to densely villous-puberulous; wood composite, a large central bundle surrounded by 3 small peripheral bundles. *Leaves* pinnately 5-foliolate, to 33 cm long; petioles 10–14 cm long, narrowly and evenly winged with a broad medial rib; rachis narrowly winged; petiole and rachis puberulent and coarsely strigose along the medial rib, sparsely strigose on the margins; leaflets elliptic to ovate-elliptic or obovate-elliptic, abruptly acuminate at the apex, narrowly acute at the base of the terminal leaflet, inequilaterally acute to obtuse and equilateral on the lateral leaflets, 9–19 cm long, 4–7 cm wide, crenate in the outer ¾ of the blade with blunt glandular teeth, the upper surface glabrous except for the coarsely strigose, prominently raised midrib, the lower surface glabrous except for the coarsely barbulate vein axils and sparse stiff straight trichomes on the midrib and major lateral veins, the reticulate venation prominent on both surfaces, the margin hyaline, sparsely strigose; stipules apparently deciduous. *Inflorescences* of solitary, axillary thyrses more than 4 cm long; rachis angular, viscidulous, villous-tomentose; bracteoles linear-lanceolate, 4–7 mm long, appressed-pubescent; pedicels to ca. 3 mm long, densely appressed-pubescent. *Flowers* not known; old calyx persisting in fruit, to 4.5 mm long, the sepals thick, densely appressed-pubescent. *Fruits* obovoid, ca. 2 cm long, rounded and apiculate at the apex, gradually tapered to the base, short-stipitate, red, without wings, longitudinally striate, sparsely long appressed-pubescent to glabrous outside, glabrous inside.

Paullinia sternii is similar to *P. bristanii*, *P. pinnata*, and *P. sessiliflora* var. *angustirachis*. It can be distinguished from *P. bristanii* by its obovoid rather than globose fruits, from *P. pinnata* by its larger flowers with thick appressed-pubescent sepals and by its short-stipitate fruits, and from *P. sessiliflora* var. *angustirachis* by its linear-lanceolate rather than ovate-triangular floral bracts.

The species is named in honor of W. L. Stern, one of its collectors. It is known only from the type collection which was made in tropical moist forest and bore mature fruits in late June.

DARIÉN: Trail between Río Escucha Ruida and Río Tuira, *Stern et al. 574* (GH, MO, US).

34. **Paullinia stipitata** Cuatr., Revista Acad. Colomb. Ci. Exacta 8: 476. 1952. TYPE: Colombia, Valle, Pacific coast between El Aguacate and Quebrada de la Yuca, 10–40 m, *Cuatrecasas 16085* (US).

Lianas; stems 3-angled, puberulent to tomentulose when young, viscidulous, becoming glabrous or nearly so in age, purplish, the wood composite, consisting of a large central strand and 3 much smaller peripheral strands. *Leaves* 10–27

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[22] *Paullinia sternei* Croat, sp. nov. Labrusca fruticosa; corpus lignosum compositum; rami 3–6-sulcati. Folia 5-foliata-pinnata, ad 33 cm longa; petiolus rhachisque alata. Thyrsi solitarii, axillares, plus quam 4 cm longi; bracteolae lineares-lanceolatae, 4–7 mm longae. Sepala crassa, dense adpressa-pubescentia, ad 4.5 cm longum. Fructus obovatus, ca. 2 cm longus, brevi-stipitatus, sine alis, glaber.

cm long, ternate-pinnately compound with 11 leaflets, the lowest set biternate; petiole, rachis and sometimes midrib puberulent to scabrid; petioles 1–11 cm long, viscidulous, margined on the upper surface, the lower rachis margined; upper rachis narrowly winged; blades ovate, narrowly elliptic, oblong-elliptic or oblanceolate, usually long-acuminate or sometimes bluntly acuminate at the apex, attenuate to rounded at the base, (2.5–)6–10.5 cm long, (1.3–)2.5–4 cm wide, nearly glabrous except for the frequently barbulate vein axils, glandular-punctate, entire to crenate above the middle; stipules lanceolate-linear, 6–10 mm long, viscidulous, puberulent or scabrid, becoming glabrous. *Inflorescences* solitary thyrses 3–10(–15) cm long, borne in leaf axils or on tendrils; rachis, pedicel and bracteole densely puberulent; bracteoles deltoid, less than 1 mm long. *Flowers* not known; outer sepals (persisting in fruit) puberulent outside, glabrous inside, the inner sepals glabrous. *Fruits* prominently stipitate, red, broadly obovate, emarginate to truncate at the apex, broadly 3-winged throughout most of their length, 1?-locular, densely puberulent to glabrate outside, tomentose inside, the body of the fruit 1.5–2 cm long, the stipe 4–7 mm long; seed 1, ovoid to ellipsoid, shiny, black, grayish-puberulent, white-arillate in the lower half.

Paullinia stipitata is distinguished by its ternate-pinnate leaves with more or less glabrous leaflets except for the barbulate vein axils and by its composite woody stems and broadly winged fruits. Juvenile plants are often more pubescent, being puberulent on the lower midrib, and they often have even the upper rachis very narrowly winged.

Seasonal behavior is poorly known. Mature fruits have been collected in December, February and April.

The species is known only from Panama and Colombia on the Pacific slope.

COLÓN: Santa Rita Ridge, *Dwyer & Gentry 9347* (MO, NY, SCZ, US); *Gentry 6110* (CAS, D, GH, K, MO, NY, PMA, US, VEN); *Lewis et al. 5270* (MO). PANAMÁ: Road to Cerro Campana, *Croat 14697* (MO). Cerro Jefe, *Croat 17359* (MO). 3 mi NE of Altos de Pacora, *Croat 22761* (MO). Road from El Llano to Cartí-Tupile, *Croat 22883* (MO); *Liesner 699* (MO, PMA); *Mori & Kallunki 3532* (GH, MO, PMA, TEX), *4090* (MO).

35. **Paullinia stipularis** Benth. ex Radlk., Monogr. Serj. 75. 1875. TYPE: Brazil, Barra do Negro (now Manaus), *Spruce 1856* (C, F, G, H, K, LE, NY, GH).

P. rubiginosa Camb. f. *setosa* Radlk., Monogr. Paull. 180, no. 21. 1896. LECTOTYPE: Brazil, *Blanchet 1599* (F).

Lianas; stems 4- or 5-costate, viscidulous, the ribs conspicuously hirsute-villous, the sulcae glabrous; wood simple. *Leaves* pinnately 5-foliolate, 15–25 cm long; petioles 3–13 cm long, without wings, narrowly canaliculate on the upper surface, hirsute especially above; rachis narrowly winged, hispid on the margins and on the raised medial rib, the wing broadest toward the apex; leaflets narrowly ovate to oblong-elliptic or obovate-elliptic, sharply acute to abruptly acuminate at the apex, attenuate to rounded at the base, 4–13 cm long, 2–7 cm wide, sharply serrate and glandular-toothed mostly in the outer half, sometimes to the lower fourth, sparsely hispid on both surfaces, the pubescence denser on the upper midrib, the reticulate venation prominulous beneath; stipules ovate to oblong-lanceolate, 7–10 mm long, conspicuously hispidulous outside, glabrate within,

prominently ciliate. *Inflorescences* paniculate, terminal or upper axillary; rachis and pedicels rufous-tomentose; bracteoles lanceolate-triangular, 2.5–4 mm long, glabrous inside, densely stiff appressed-pubescent outside; pedicels slender, to ca. 2 mm long, articulate about midway. *Flowers* cream-colored; buds ca. 1.5 mm long, globose; outer sepals densely appressed-pubescent, rounded, the inner ones glabrous; petals obovate, the scales with the crest obcordate, the deflexed appendage ciliate; staminate flowers with the filaments glabrous, the pistil sharply 3-angled, hispidulous on the angles. *Capsules* ellipsoid, 3-angular, ca. 1.5 cm long, orange (fide *Duke 14491*), sparsely hispidulous outside, wooly tomentose inside; seeds not seen.

This is the first report for the species outside of Brazil. In Panama *Paullinia stipularis* has been collected only in premontane wet forest and tropical wet forest. Flowering occurs during the mid to late rainy season with fruits maturing mostly by the late rainy season.

COCLÉ: Between Cerro Pilón and El Valle, *Duke & Dwyer 13912* (MO, SCZ, US). DARIÉN: Río Tuquesa at middle elevation, 250 m, *Mori 7096* (MO). PANAMÁ: Between Cañasas and Sabalo, *Duke 14491* (MO).

36. **Paullinia tenuifolia** Standley ex Macbride, Field Mus. Nat. Hist., Bot. Ser. 13: 359. 1956. TYPE: Peru, Loreto, Iquitos, Fundo Indiana, *Mexia 6394* (F, US).

P. toxicodendroides Steyermark, Bol. Soc. Venez. Ci. Nat. 26: 400. 1966. TYPE: Venezuela, Distrito Federal, Cerro Naiguata, 1000–1300 m, *Steyermark 92079* (US)

Lianas; stems several-angled to terete when young, weakly viscidulous, sparsely hispidulous on the angles, terete to weakly 3- or 4-sulcate in age; wood simple. *Leaves* pinnately 5-foliolate, 10–20(–27) cm long, thin, almost glabrous; petioles without wings, 2–5 cm long, canaliculate above, nearly glabrous except along the upper margins; rachis margined with a medial ridge, the margins and ridge scabridulous; leaflets lanceolate-elliptic, ovate-lanceolate to narrowly-elliptic, narrowly long-acuminate at the apex, attenuate to obtuse or acute at the base, (2.2–)4–15 cm long, 0.7–5(–6.4) cm wide, crenate-serrate in the outer ¾ with weakly glandular teeth, sparsely ciliate, the upper surface glabrous except hispidulous on the sharply raised upper midrib, the lower surface glabrous except for occasional stiff trichomes on the major veins and barbulate vein axils, the major lateral veins 6–10 pairs, mostly extending to or near the margin; stipules nearly linear, to 7 mm long, glabrous except for the sparsely ciliate margins. *Inflorescences* of usually several (rarely 1) elongate thyrses borne at leafless nodes, branched from so near the base as to appear fasciculate, the branches to 11 cm long; rachises slender, short-villous to puberulent, viscidulous; pedicels and calyces puberulent. *Flowers* white, crowded on the rachis; outer sepals to 1.5 mm long, ciliate; petals oblong-elliptic, ca. 3 mm long, glabrous, the anterior scales with the basal part rounded, ca. 1.3 mm long, prominently ciliate on the margin, the crest oblong-linear, as long as the basal part, the lateral scales also with a single slender crest; disc glands 4, equal, ovoid or semicircular, whitish, puberulent on the inner edge; bisexual flowers with the stamens ca. 1.5 mm long, the filaments

flattened, puberulous throughout, the pistil 2.3 mm long, the ovary ovoid to rounded, bluntly trigonous, sparsely hispidulous and glandular, 0.6 mm long, the style ca. 3 times as long as the ovary, 3-branched in the upper fourth, glabrous except for the stigmatic papillae. *Fruits* obovoid, rounded to weakly emarginate at the apex, obtusely tapered to a sessile base, 12–15 mm long, to ca. 8 mm wide, 1-locular, inconspicuously and faintly short-puberulent, glandular, red; seed 1, globose, densely puberulent, borne upon a thick white aril.

Paullinia tenuifolia is recognized by its thin, 5-foliolate-pinnate leaves with wingless petioles and rachises, by its slender, apparently fasciculate thyrses, flowers with single slender scale crowns, and small wingless fruits. Flowers of the species are similar to those of *P. buricana* but that species has ternate-pinnate leaves with winged rachises.

Flowering apparently occurs in the dry season in February. Mature fruits have been collected in November.

Paullinia tenuifolia ranges from Panama to Venezuela, Peru, and Brazil (Acre). It is known from tropical wet forest in westernmost Panama.

CHIRIQUÍ: San Bartolo Límite, 400–600 m, *Busey 562* (MO, PMA). 10–11 mi W of Puerto Armuelles, 300–500, *Croat 21979A* (MO).

37. **Paullinia turbacensis** H.B.K., Nov. Gen. Sp. Pl. 5: 114. 1821. TYPE: Colombia, near Turbaco, *Humboldt & Bonpland 1431* (P).—FIG. 9.

P. wetmorei Standley, Contr. Arnold Arbor. 5: 96. 1933. TYPE: Panama, *Shattuck 689* (F, holotype; MO, isotype).

Tendrilled *lianas*; stems terete, glabrate with conspicuous brown lenticels; wood simple; sap at periphery milky, not copious. *Leaves* 3-foliolate; petioles to 14 cm long, with marginal ribs above, glabrate; leaflets broadly elliptic to ovate, acuminate or acute at the apex, attenuate to rounded at the base, 5–15 cm long, 3–12 cm wide, to 23 cm long and 11 cm wide as juveniles, glabrate except for the axillary tufts beneath, subentire to remotely crenate-dentate. *Inflorescences* to 7 cm long, solitary or clustered at the nodes, often on leafless stems near the ground but also occurring to 5 m high. *Flowers* white, ca. 5 mm long, in small helicoid thyrses; sepals appressed-pubescent; petals oblong, to 4.5 mm long, the scales ca. ⅔ as long as petals, yellow-crested, those of the anterior petals bilobed, their deflexed appendages pubescent, the disc glands white, acute, densely pubescent; staminal cluster equalling the petals, the filaments densely pubescent throughout; nectar abundant, stored in the vicinity of the anterior disc glands; ovary glabrous, the styles pubescent. *Capsules* elliptic to obovate, 2 cm long, red, 3-locular, short-pubescent, the 3 boat-shaped valves broadly spreading to expose seeds; seeds 1–3, black, shiny, less than 1 cm long, covered on the lower half by a fleshy white aril, dangling on a thin funiculus when fully displayed.

The species is confused with no other species in Panama. It is distinguished by its 3-foliolate leaves, conspicuously lenticellate stems, and pubescent, distally winged capsules.

Paullinia turbacensis flowers in Panama mostly in the early dry season from November to February. Fruits mature from February to April.

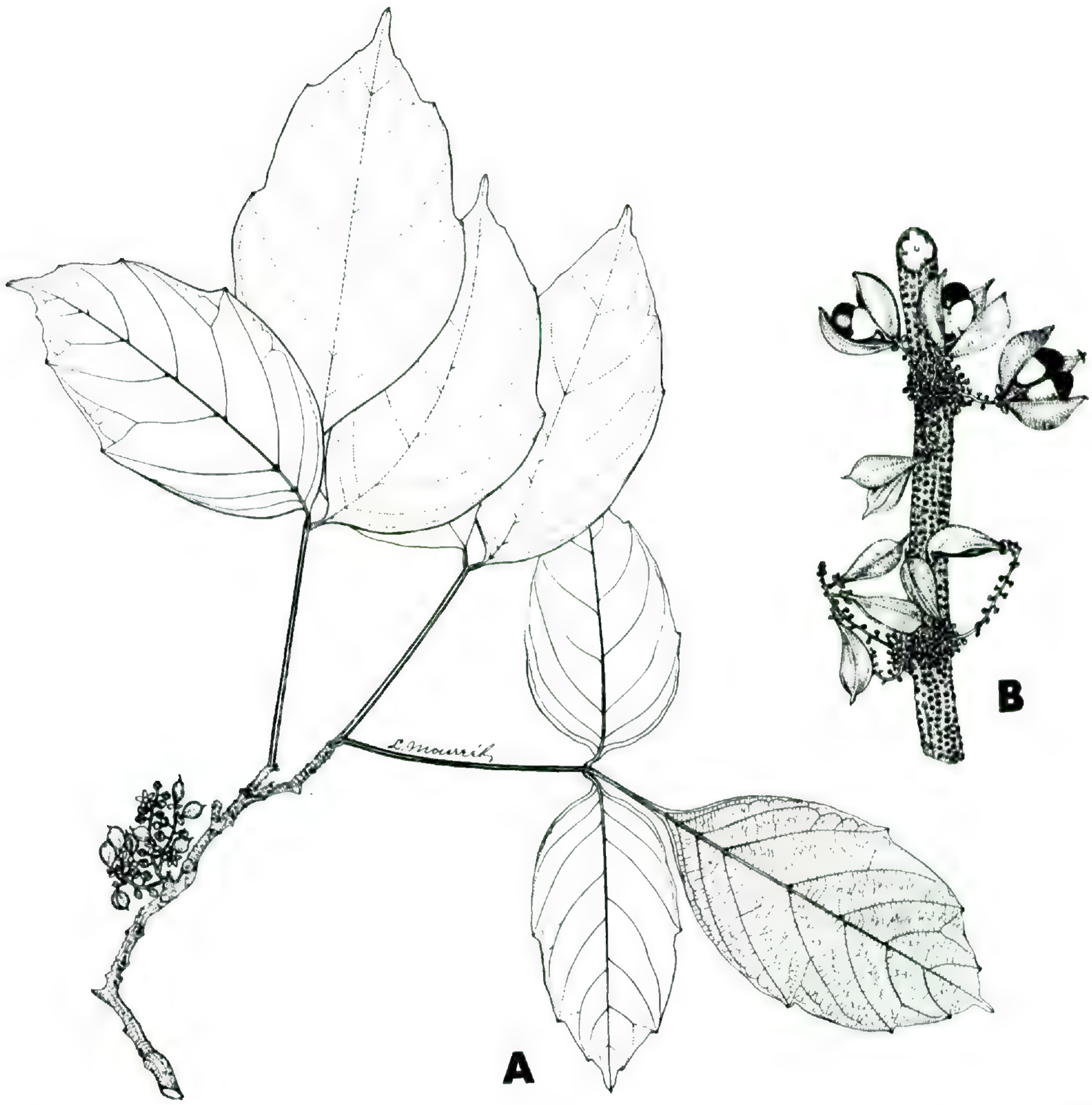

FIGURE 10. *Pseudima frutescens* (Aubl.) Radlk.—A. Sterile branch (×⅖). [After *Bristan* (×3/10).—B. Mature fruits (×3/10). [After *Croat 7069* (MO).]

It is known from Mexico, Guatemala, Panama, and Colombia. In Panama it is known from tropical moist forest and premontane wet forest.

CANAL ZONE: Barro Colorado Island, *Brown 1* (F); *Busey & Croat 245* (MO); *Croat 4279* (DUKE, F, MO, NY, SCZ), *4309* (MO), *4553* (F, MO, NY, SCZ), *4609*, *4665* (both MO), *7069* (MO, NY, SCZ), *7093*, *7213*, *7324*, *7669* (all MO), *7817* (MO, SCZ), *7900*, *7927*, *8114* (all MO), *8236* (MO, SCZ), *16213A* (MO); *Foster 679* (DUKE), *1443* (DUKE, PMA); *Gentry 426* (WIS); *Graham 193* (GH, MICH); *Hladik 91* (MO); *Hunnewell 1443* (DUKE, GH); *Killip 39973* (MO, US); *Oppenheimer* (MO); *Robyns 65–8* (MO); *Shattuck 609* (F, MO, US); *Shattuck 689* (F, MO); *Standley 31246*, *41095* (both US); *Stoutamire 2052* (MICH); *Wetmore & Abbe 21A* (F); *Woodworth & Vestal 640* (A, F, MO). Colón to Empire, *Crawford 434* (F, NY). Quebrada Tranquilla, *Dodge & Allen 17327* (MO). Madden Dam, *Dwyer & Robyns 14* (MO). Río Providencia and ridge S of river, 5–170 m, *Gentry & Nee 8704* (F, MO, PMA). Maume Station on Panama Rail Road, *Hayes 499* (K). Near Bohio, 10–20 m, *Maxon 4773* (M, NY, US). 2–3 km N of Gamboa, 30–200 m, *Nee 9447* (MO, PMA). Boy Scout Road, *Dwyer 8386* (MO, SCZ); *Porter et al. 4043* (MO, SCZ). Near Gatún, *Standley*

27190 (US). Vic. of Fort Sherman, *Standley 31048* (US). Darién Station, *Standley 31601* (US). CHIRIQUÍ: Rabo de Puerco, 9 km along road W to Puerto Armuelles, *Busey 705* (MO). Burica Peninsula along quebrada near Punta de Piedra, *Croat 22442* (MO). 6 mi S of Puerto Armuelles, *Liesner 418* (MO). COLÓN: Top of Tumba Vieja, *Dodge et al. 16934* (G, K, MICH, MO, P). Between France Field and Cativa1, *Standley 30377* (US). DARIÉN: Cerro Pirique, *Duke 8084* (MO). Río Sambú, 0–5 mi above Río Venado, *Duke 9278* (MO). Hydro Camp, Pico Pendejo, on Río Sabana, *Duke 15455* (MO). Trail from Pucro to Cerro Mali, 150–500 m, *Gentry & Mori 13542* (MO, PMA). North slopes of Cerro Pirre, 300–700 m, *Mori & Kallunki 5377* (MO). Without exact locality, *Seemann 3841* (K). PANAMÁ: Above Campana, 600–800 m, *Allen 1323* (MICH, MO). 1 mi E of El Llano, *Croat 14501A* (MO). Without exact locality, *Sexton s.n.* (MO). Road to Cerro Azul, 4 km above Pan-Am. Hwy., *Vargas 17* (MO, PMA). SAN BLAS: Perme, *Cooper 237* (F).

11. PSEUDIMA

Pseudima Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8: 300. 1878. TYPE: *Sapindus frutescens* Aubl. = *Pseudima frutescens* (Aubl.) Radlk.

Polygamous *shrubs* or small *trees*; trunks slender. *Leaves* large, pinnate; leaflets 10–18, opposite or subopposite, oblong to oblong-lanceolate or elliptic, pinnately veined, entire, petiolate, exstipulate. *Inflorescences* of terminal or subterminal panicles. *Flowers* regular; sepals 5, free, concave in 2 unequal imbricate series, the 2 exterior sepals ovate, smaller, the inner sepals elliptic; petals 5, lanceolate to linear, lacking scales within; disc cupular or plate shaped, 5-angled; stamens 8, borne within the disc, erect, about equalling the petals in staminate flowers, exceeding the ovary but shorter than the petals in bisexual flowers, the filaments filiform, the anthers ovate-oblong; ovary 2-(rarely 3-) locular, 2-(3-) coccate-lobate, the style borne between the two lobes of the fruit, remaining basal in fruit where one lobe aborts. *Capsules* obcordate or obovate with an aborted basal lobe, stipitate, the valves coriaceous; seeds ellipsoid or obovoid, black, shiny, minutely punctate, the aril white, basal, inconspicuous; embryo curved.

The genus has three species.

1. **Pseudima frutescens** (Aubl.) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 8: 300. 1878.—FIG. 10.

Sapindus frutescens Aubl., Hist. Pl. Guian. 1: 355, *tab. 138*. 1775. TYPE: French Guiana (not seen).

Shrubs or *trees* 3–6 m tall; trunks slender, sometimes clustered; stems terete, weakly striate, densely appressed-puberulent. *Leaves* paripinnate, 30–70 cm long; petioles terete, 4–10 cm long; rachises terete, glabrous, the epidermis usually with a 1-celled, grayish, sometimes exfoliating layer; petiolules 1–1.5 cm long, marginally ribbed above; leaflets 6–9 pairs, leaflets narrowly oblong to oblong-oblanceolate, acute to gradually or bluntly acuminate at the apex, acute to attenuate and often inequilateral at the base, (5.5–)10–30(–40) cm long, (1.5–)4.5–7(–10) cm wide, glabrous, the major lateral veins often arising from the midrib at an angle of 80–90°. *Inflorescences* terminal panicles, the branches densely strigose, the smaller ones drying angulate. *Flowers* white; pedicels and

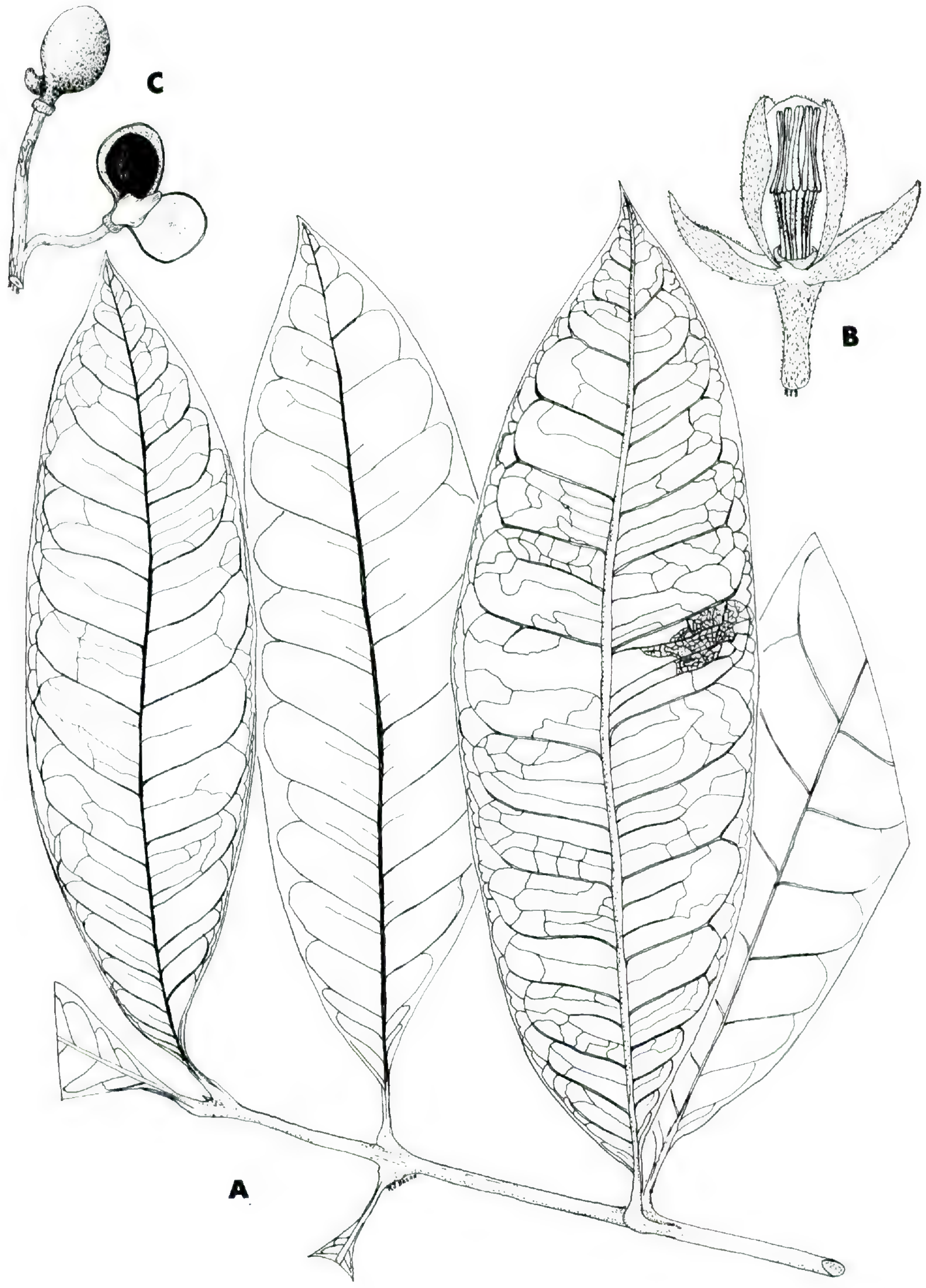

FIGURE 10. *Pseudima frutescens* (Aubl.) Radlk.—A. Sterile branch (×⅖). [After *Bristan 1354* (MO).]—B. Staminate flower (×4⅗). [After *Duke 8603* (MO).]—C. Fruit (×⅖). [After *Bristan 1354* (MO).]

calyces densely strigose without, glabrous within; sepals ovate, the outer to 3.5 mm long, the inner to 4.5 mm long; petals obovate, 3.5 mm long, rounded at the apex, thickened and nearly clawed at the base, sericeous without, sparsely long-pubescent within, especially midway; disc plate shaped, glabrous, the margin elevated with 5 lobes, these alternating with the petals; staminate flowers with the stamens 3.5 mm long, the filaments conspicuously long white-pubescent in the upper ⅔, glabrous below, the anther 1.5 mm long, oblong, the pistil ca. 0.4 mm long, lenticular, glabrous, the styles 2, thick, about as long as the ovary; pistillate flowers (Guyana) with the stamens ca. 2 mm long, the pistil 2.5 mm long, the ovary broadly ovate, 2-carpellate, ca. 1.5 mm long, glabrous except along the hispid upper margins, the style ca. 1 mm long, hispid, blunt at the apex. *Capsules* red, 2.2–2.7 cm long (including the stipe), prominently obcordate when both sections develop, or obovate with a small aborted lobe at the base, the lobes to 2 cm diam., the texture of the outer valve surface minutely warty, dull, drying brick red, the inner valve surface shiny, reddish brown; seeds obovoid, 1.5–1.8 cm long, black, shiny, minutely puncticulate, completely glabrous at the point of attachment.

Pseudima frutescens is distinguished from other Sapindaceae in Panama by its large, red, 2-valved fruits and large, shiny black seeds. It is apparently closely related to *Pseudima costaricensis* described from Palmar Norte in southeastern Costa Rica but that species differs in having much smaller, lighter-colored leaves.

Flowering is known from August. Collections with mature fruits have been made in October and December. *Duke 387* records that the fruits have a bad taste.

Pseudima frutescens ranges from Panama to the Guianas and Brazil.

DARIÉN: Bolamina, *Duke 386* (MO, US). Río Chucunaque, between Río Membrillo and Río Subcutí, *Duke 8603* (MO, US). Río Aruza, *Bristan 1354* (MO). SAN BLAS: Mainland opposite Ailigandí, *Lewis et al. 168* (MO).

12. SAPINDUS

Sapindus L., Sp. Pl. 367. 1753; Gen. Pl., ed. 5. 171. 1754. TYPE: *S. saponaria* L.

Electra Noronha, Verh. Batav. Genootsch. Kunsten 5: 2. 1790, non DC., 1836, nec Panzer, 1813. TYPE: not indicated.

Dittelasma Hook. in Benth. & Hook., Gen. Pl. 1: 395. 1862. TYPE: *D. rarak* (DC.) Hieron. = *Sapindus rarak* DC.

Polygamous *shrubs* or small *trees*; stems glabrous or subtomentose. *Leaves* pinnate, exstipulate, petiolate, with a narrowly winged or wingless rachis; leaflets opposite or alternate, petiolulate or sessile, elliptic or ovate-lanceolate, entire, membranous or chartaceous. *Panicles* large, terminal, divaricately branched; bracteoles minute. *Flowers* white, short-pedicellate, often regular, obliquely symmetrical, small; sepals 5, orbicular or ovate, concave, imbricate, the outer 2 smaller; petals usually 5, subglabrous or pubescent outside, with a short scale above the claw on the inside, the scale barbate; disc usually regular, glabrous or pilose; stamens 8, exserted, pilose at the base; ovary 3-lobed, 3-locular, the style

subulate or shortly filiform, the ovules singular in each locule. *Fruits* drupaceous, indehiscent, with 3 or 2 (1) cocci, carnose or coriaceous, the cells oblong or globose; seeds usually globose, without an aril.

The genus has about 13 species in tropical and warm temperate areas of both hemispheres. Most species have been described from the Old World. It is quite likely that the species treated below is the only one to be found in the American tropics. Radlkofer (1933–1934) segregated two other species in Mexico and the southern United States but these are doubtfully separable.

1. **Sapindus saponaria** L., Sp. Pl. 367. 1753. TYPE: Brazil or Jamaica, Herb. Linn. 514.1 or 514.2 (LINN, not seen, MO, microfiche).—FIG. 11.

S. rigidus Miller, Gard. Dict., ed. 8. 2. 1768. TYPE: Mexico, Vera Cruz, *Houstoun* (not seen).
Cupania saponarioides Swartz, Prodr. Veg. Ind. Occ. 62. 1788. TYPE: West Indies (not seen).
Sapindus indica Poir. in Lam., Encycl. Méth. 6: 667. 1804. TYPE: West Indies (not seen).
S. forsythii DC., Prodr. 1: 607. 1824. TYPE: in arenosis maritanus insulae Granatae (not seen).
S. stenopterus DC., Prodr. 1: 607. 1824. TYPE: Santo Domingo, *Bertero* (not seen).
S. inaequialis DC., Prodr. 1: 608. 1824. TYPE: Guadelupe, *Bertero* (not seen).
S. divaricatus Cambess. in St.-Hilaire, Fl. Bras. Mer. 1: 300. 1828. TYPE: Brazil, Minas Gerais, prope Sabana (not seen).
S. turczaninowii Vidal, Sinop. Fam. Atlas. 21. *tab. 34.* 1833. TYPE: not seen.
S. thurstonii Rock, Bot. Bull. Board Commiss. Agric. Forest. Hawaii 1: 1911. TYPE: Sandwich Islands (not seen).

Trees 3–17(–23) m tall, to 18 cm d.b.h.; stems sulcate, glabrous to puberulent. *Leaves* pinnate, 10–30(–57) cm long; leaflets 5–10, narrowly lanceolate to oblong, unequal, obtuse to long-acuminate at the apex, acute or obtuse to attenuate at the base, entire, membranous to somewhat coriaceous, 5–13(–20) cm long, 3–5(–7.3) cm wide, glabrous or subglabrous; rachis sulcate, marginally ribbed or winged; petioles winged or wingless. *Panicle* terminal, 15–25 cm long, the branches and pedicels densely puberulent to tomentose; pedicels 0.5–1.5 mm long, articulate above the middle. *Flowers* white; sepals rotund or elliptic, puberulent, ciliolate, ca. 3 mm long; petals ca. 1.5 mm long, ciliolate, glabrous without, villous at base within; disc fleshy, spreading, glabrous; stamens exserted, to ca. 3 mm long, the filaments filiform, villous to about midway; ovary ovate, 3-lobed, glabrous. *Fruit* of 1–3 cocci; cocci brown to yellow, globose, glabrous, ca. 1.5 cm diam., shiny, often lenticellate at maturity, the surface smooth; seeds globose, 1.2 cm diam., set at the base of the carpel in a cottony mat of pubescence.

Sapindus saponaria is distinguished from other Sapindaceae in Panama by being arborescent, pinnately leaved, and having indehiscent 2- or 3-lobed fruits.

Flowering occurs from November to January in Panama. Fruits develop to mature size by February and are apparently all dispersed before July.

The species ranges from southern Florida to the West Indies and Argentina. It has been introduced into tropical areas of Africa and Asia. In Panama it is known from lower montane rain, premontane wet, tropical moist, premontane moist and tropical dry forests.

Common names for the species include "limoncillo," "jaboncillo," and "soap-

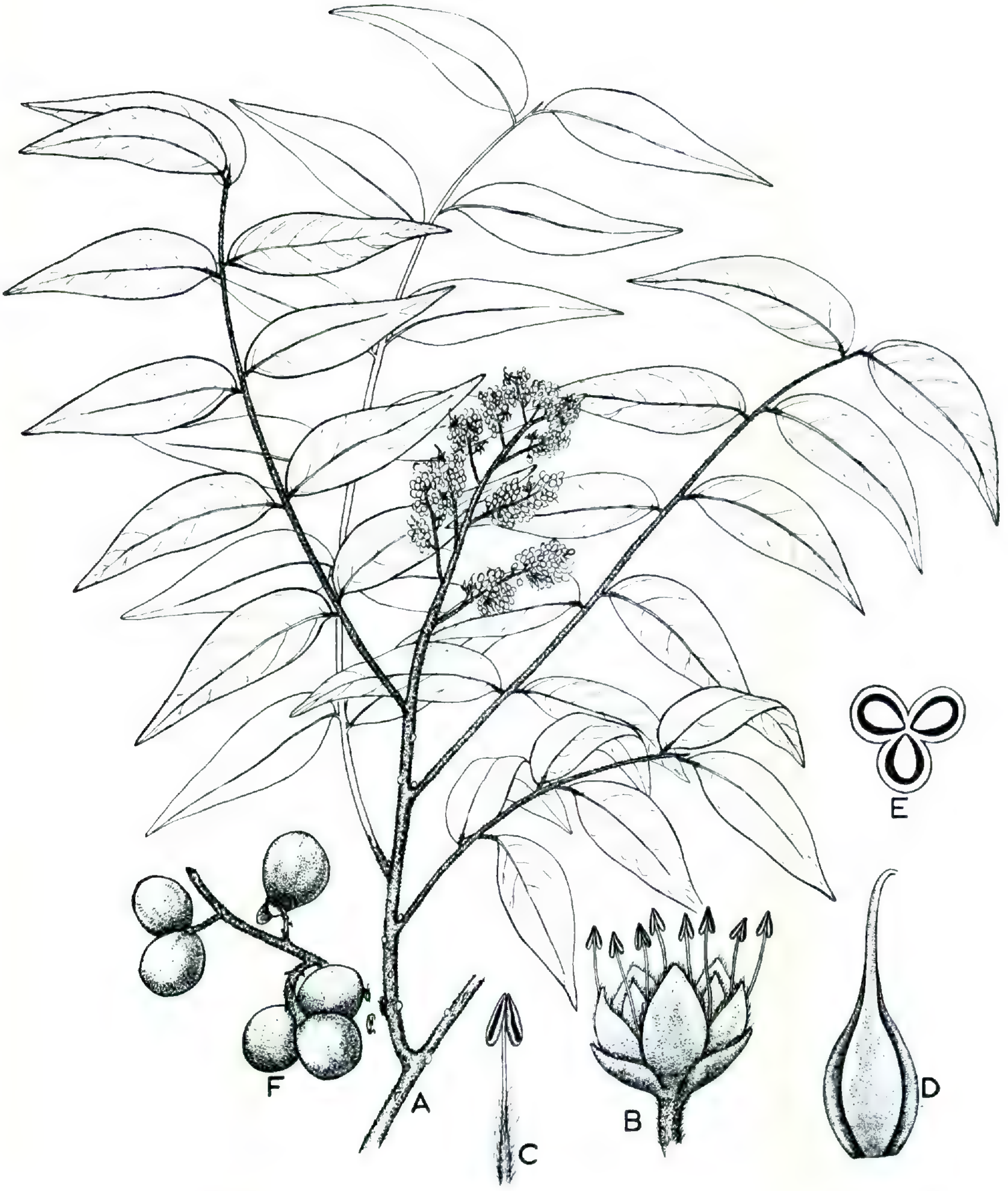

FIGURE 11. *Sapindus saponaria* L.—A. Flowering branch (×½). [After *Liesner 1191* (MO).]—B. Staminate flower (×7½).—C. Stamen (×15).—D. Pistil (×9).—E. Ovary cross-section. [After *Gaumer 2339* (MO), Mexico.]—F. Fruit (×½). [After *Hinton 5785* (MO), Mexico.]

berry." When crushed and rubbed with water the fruits produce a lather, and they have been used as a substitute for soap. Standley (1928) reports that the fruits contain as much as 30% saponin.

CANAL ZONE: Gaillard Hwy., ca. ½ mi from Gamboa Road, *Correa et al. 662* (DUKE, PMA, SCZ) Radar Road N of Summit Garden, *Croat 9084* (MO, SCZ). Summit Gardens,

Croat 12649 (DUKE, F, MO, SCZ). 1 mi N of Paraíso, *Croat 12650* (DUKE, F, MO, SCZ). Gaillard Hwy. near Continental Divide, *Croat 13260* (MO, SCZ). Near Madden Dam, *Dodge 16559* (MO). Farfan Beach, *Dwyer 2603, 3057* (both MO). Curundú, *Dwyer 3481* (MO). Cocoli, *Dwyer 7216* (GH, MO, US). 3 mi N of Gamboa, *Gentry 2823* (DUKE, MO, S). 2 mi W of Thatcher Ferry Bridge, *Lazor 2201* (MO, SCZ). Farfan Beach, *Tyson & Blum 2603* (SCZ). CHIRIQUÍ: Cerro Horqueta, NW of Boquete, *Dwyer et al. 541* (MO). COCLÉ: Capellania, Natá, *Gonzalez 3* (MO, PMA). Hills NE of El Valle, *Lewis et al. 1689* (GH, MO). DARIÉN: Bolamina, *Duke & Bristan 386* (MO). HERRERA: vic. of Chitré, *Allen 1098* (F, MO, US). PANAMÁ: Vic. of Pacora, *Allen 2030* (MO, US). 1 mi E of Tocumen, *Blum & Tyson 1967* (SCZ). Headwaters of Río Corso, *Duke 11923* (MO). Jaboncillo, Montigo Bay area, *Fischer 12* (F). SAN BLAS: Río Sugandi across from Ustupo-Concepción Island, *Mori 389*.

13. SERJANIA

Serjania Miller, Gard. Dict., abr. ed. 4. 1754. TYPE: *Paullinia seriania* L. = *Serjania sinuata* (Lam.) Schum.

Polygamous, tendrilled *lianas* or scandent *shrubs*; stems terete to prominently ribbed, the wood simple or composite, usually with 3 or more peripheral bundles, these solitary or paired, terete or flattened, regular or irregular; tendrils axillary or peduncular, forked, often bracteate at the fork, the arms coiled like a watch-spring. *Leaves* 3-foliolate, biternate or decompound-ternate, with minute stipules or none, often pellucid-punctate. *Thyrses* arranged in axillary or terminal racemes or panicles. *Flowers* small, irregular; sepals 4 or 5, persistent, 2 sometimes united, the outer ones smaller; petals 4, with a complex crested scale within, the scale usually ½–¾ as long as the petal, the scales of the anterior petals larger than those of the lateral petals, the crest usually orange or yellow and variously shaped, bearing within a deflexed, usually barbed appendage which often extends over the disc glands at the base, the lateral inner margins of the deflexed appendages usually coherent by means of their intertwining trichomes; disc glands 2–4, white or yellow, the lateral ones smaller or reduced altogether; stamens 8, unequal, the 3 adjacent to the anterior petals smaller, the staminal cluster eccentric, the filaments connate at the base; ovary sessile or short-stipitate, 3-celled, the style 3-lobed, the ovules solitary, affixed below the middle of the cell. *Fruits* usually ovate-cordate, consisting of 3 samaras, broadly winged toward the base, finally separating from a central axis; seeds sometimes short-arillate with crustaceous testa; embryo incurved, the cotyledons plicate.

About 215 species are known, ranging from the southern United States to tropical South America.

a. Leaves 3-foliolate (ternate) or bipinnately compound.
  b. Leaves 3-foliolate.
    c. Stems and leaves glabrous ..... 4. *S. circumvallata*
    cc. Stems and leaves densely rufous tomentose-pilose ..... 8. *S. grandis*
  bb. Leaves bipinnately compound.
    d. Leaves at most 3-pinnate; leaflets more than 3 cm wide ..... 10. *S. mexicana*
    dd. Leaves often 4- or 5-pinnate; leaflets less than 2 cm wide ..... 15. *S. trachygona*
aa. Leaves biternate (3 sets of 3 each).
  e. Rachis usually winged.
    f. Seed-bearing part of fruit glabrous (fruits unknown in *S. darcyi*); larger stems armed with short spines; wood simple.

g. Stems deeply sulcate with composite wood, the central core usually surrounded by 5 peripheral bundles, the ribs often armed with short prickles; flowering in the early dry season; plants of lowland regions ..... 10. *S. mexicana*
gg. Stems terete, unarmed, the wood simple; flowering in the rainy season (August); plants of higher elevations (to 1,800 m) ..... 6. *S. darcyi*
ff. Seed-bearing part of fruit conspicuously pubescent; stems unarmed; wood simple or composite.
h. Lower surface of the leaflets glabrous; leaflets, flowers and fruits sometimes with conspicuous dark lines.
i. Cells of the fruit whitish-hirtellous; lower leaflet surfaces, flowers, and fruits with conspicuous dark black lines; peripheral vascular bundles usually flattened, irregular, often more than 1 mm wide ..... 3. *S. atrolineata*
ii. Cells of the fruit brown-hispid; lower leaflet surfaces, flowers, and fruits without conspicuous black lines; peripheral vascular bundles usually terete, regular, usually less than 1 mm wide ..... 12. *S. paucidentata*
hh. Lower surface of the leaflets at least sparsely pubescent; leaflets, flowers, and fruits lacking dark lines.
j. Leaflets conspicuously pubescent above, densely hirtellous to short-pilose beneath, the vein axils not conspicuously more pubescent than the surface; flowering in the early dry season; plants of lower elevations ..... 14. *S. rhombea*
jj. Leaflets nearly glabrous above, sparsely hirtellous beneath, the vein axils densely pubescent; flowering in the rainy season (August); plants of elevations to 1,800 m ..... 6. *S. darcyi*
ee. Rachis wingless.
k. Cells of fruits and ovaries glabrous or essentially so.
l. Stems glabrous and shiny; leaflets glabrous beneath except for the usually barbulate vein axils ..... 13. *S. pluvialiflorens*
ll. Stems densely pubescent (at least beneath the inflorescences); leaflets hispidulous or scabridulous throughout beneath (at least on the major lateral veins), usually not barbulate in the vein axils.
m. Fruits about as broad as long; leaflets subentire to remotely crenate in the outer half of the blade, mostly more than 8 cm long and 4 cm wide, the teeth eglandular or with the gland inconspicuous; flowering in November and December; plants of disturbed situations in drier parts of tropical moist and premontane moist forests. ..... 9. *S. insignis*
mm. Fruits much longer than broad; leaflets lobate-crenate, mostly less than 7 cm long and 4 cm wide, the teeth with a conspicuous reniform gland; flowering in August and September; plants of premontane wet and tropical wet forests ..... 2. *S. allenii*
kk. Cells of fruits or ovaries conspicuously pubescent.
n. Lower leaflet surfaces densely and conspicuously pubescent, the trichomes usually reddish brown.
o. Flowers ca. 7 mm long; fruits more than 3.5 cm long, subrectangular-oblong, the cell conspicuously brown-hispid, the trichomes ca. 2 mm long, each cell bearing a sharp horn ..... 5. *S. cornigera*
oo. Flowers less than 5 mm long; fruits less than 2.5 cm long, ovate-cordate, the cell densely matted with whitish, often appressed, soft trichomes, not brown-hispid, the trichomes very short, the cells not at all horned ..... 1. *S. acuta*
nn. Lower leaflet surfaces glabrous or only sparsely pubescent, any trichomes not reddish brown.
p. Upper leaf rachis conspicuously margined; lower leaflet surface with conspicuous blackish lines visible to the naked eye ..... 3. *S. atrolineata*
pp. Upper leaf rachis not conspicuously margined; lower leaflet surface lacking conspicuous blackish lines visible to the naked eye.
q. Vein axils of the lower leaflet surface barbulate; stems 5-ribbed and with 5 peripheral bundles; fruits constricted below the seed-

bearing part; anterior scale crests of the petals deeply bifid ..... 11. *S. paniculata*

qq. Vein axils of the lower leaflet surface not barbulate; stems usually weakly 10-ribbed and with 10 peripheral bundles; fruits not at all constricted below the seed-bearing part; anterior scale crests not deeply bifid ..... 7. *S. decapleuria*

1. **Serjania acuta** Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 349. 1862. TYPE: Panama, *Seemann 1644* (BM, K).

S. seemannii Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 346. 1862. TYPE: Panama, *Seemann 1210* (BM, K).

S. velutina var. *foliis pellucido-punctatis* Seem., Bot. Voy. Herald 92. 1857, polynomial, nom. nud. TYPE: Panama, *Seemann* (based on same as *S. seemanii* Triana & Planch.).

S. salzmanniana Seem., Bot. Voy. Herald 92. 1857, non Schlecht., 1844. TYPE: Panama, *Seemann 1644* (BM, GH).

S. sordida Radlk., Monogr. Serj. 272. 1875. TYPE: Mexico, *Née* (Herb. Pavon, not seen).

Tendrilled *lianas*; stems 6-costate, usually rufous-villous; wood simple. *Leaves* biternate; petiole 2–5 cm long; petiole and rachis without wings; leaflets elliptic or elliptic-lanceolate to oblong or ovate-lanceolate, acuminate at the apex, obtuse or attenuate at the base, 1.5–11 cm long, 1–5 cm wide, entire or with small teeth above the middle, subcoriaceous, villous to rufous-tomentose beneath, glabrate to sparsely pubescent on the upper surface, densely pubescent on the major veins, the midrib and major lateral veins sharply raised above, the surface shiny, viscidulous; stipules ovate to triangular, minute. *Thyrses* solitary in the axils of the leaves, on tendrils, or in terminal panicles less than 12 cm long, rufous-tomentose; bracteoles acute; pedicels 2–3 mm long. *Flowers* white, 3–4 mm long; sepals ovate, densely rufous-tomentose, 2–5 mm long; petals oblong-obovate, glabrous without, sparsely glandular within, 2.5–3.5(–4.5) mm long, the scale 2–3 mm long, marginally ciliate, the crest orange, emarginate to prominently bifid with the projections usually acute, the deflexed appendage densely villous throughout; stamens about as long as the scales of the petals, the filaments villous; ovary 3-lobed, tomentose. *Fruits* ovate-cordate, 2–2.5 cm long, to 2 cm wide, the cells to ca. 4 mm wide, densely whitish-puberulent, viscidulous, the wings shiny, puberulent at least along the inner edge, constricted at the lower edge or below the seed-bearing part.

Serjania acuta is most easily confused in Panama with *S. insignis* and *S. decapleuria* but is distinguished by its densely rufous-tomentose flowers, densely pubescent lower leaflet surfaces, and its usually acutely bifid scale crests on the anterior petals.

The species flowers from January to April. Fruits mature from March to May.

Serjania acuta ranges from Mexico to Panama and Venezuela, usually at elevations of 1,000–1,500 m. In Panama, it is known only from premontane wet forest in Chiriquí Province.

CHIRIQUÍ: Bajo Mono, *Davidson 576* (A, F, MO). Boquete, 1000–1300 m, *Pittier 2961* (GH, M, NY, US). Volcán de Chiriquí, *Seemann 1644* (BM, GH). VERAGUAS: Without exact *locality, Seemann 1049* (K). *Seemann 1210* (BM, K).

2. **Serjania allenii** Croat.[23] TYPE: Panama, *Croat 27085* (MO-2199339, holotype; F, K, PMA, RSA, VEN, US, isotypes).

Tendrilled *lianas*; stems terete, viscidulous, weakly ribbed, the ribs conspicuously villous, the sulcate regions glabrous to sparsely pubescent, often with raised, dark orange glands; wood simple. *Leaves* biternate; petiole 1.5–7 cm long; petiole and rachis margined with a prominent medial rib; petiole, rachis, and petiolules villous; leaflets ovate to ovate-elliptic, gradually to abruptly acuminate, the acumen often rounded at the apex, obtuse to attenuate at the base, 1–7 cm long, 0.8–4 cm wide, sparsely scabridulous or hispidulous above and beneath, especially on the major veins, shiny above, the midrib and major lateral veins prominently raised, duller and viscidulous beneath, both surfaces with brown or orange glands, the margin bluntly lobate-crenate above the middle, the teeth reflexed with a large reniform gland. *Thyrses* in upper axillary or terminal panicles ca. 15 cm long; pedicels 1–2 mm long, articulate in the lower fourth. *Flowers* 3–4 mm long; calyx 1.5–2.5 mm long, glabrous except for the villous margin; petals narrowly-obovate, to 3 mm long, glabrous, sometimes glandular within, the anterior scales 1.5–2 mm long, villous along the margins and at the base of the subtending disc gland, the crests very short, emarginate, orange, the deflexed appendage ca. 1 mm long, usually glabrous along the outer margins, densely villous along their common inner margins; filaments villous in the lower ½–⅔; bisexual flowers with the stamens to ca. 1.5 mm long, the ovary glabrous, brown-glandular, trigonous, slightly longer than the stamens; staminate flowers with the stamens to 3 mm long, the pistil very reduced. *Fruits* narrowly ovate (to narrowly oblong in immature fruits), ca. 3 cm long and 1.8 cm wide, weakly cordate at the base, the sinus 1–3 mm deep, scarcely or not at all constricted beneath the seed-bearing part, glabrous, viscidulous, the veins prominent.

Serjania allenii is distinguished by its biternate, viscidulous leaves with nude rachises and petioles, and by its raised, orange to brown glands on the lower leaflet surfaces. It can also be distinguished by its unusually narrow, glabrous, viscidulous fruits. The species is most easily confused with S. *pluvialiflorens* but differs in sparsely pubescent lower leaflet surfaces, densely villous stems, smaller flowers with ovate rather than oblong disc glands, and appendages of the anterior scales villous only along their common inner margin. The deflexed appendages of S. *pluvialiflorens* are villous throughout.

Like S. *pluvialiflorens*, this species is unusual for flowering in the rainy season. It flowers in August and September. Fruits are probably mature by October. S. *allenii* is endemic to Panama.

CANAL ZONE: Pipeline Road, *Gentry 1796* (MO, NY, PMA, SCZ), *1948* (DUKE, GH, MO, NY, SCZ). COCLÉ: Hills N of El Valle, *Allen 2710* (MO). Between Cerro Pilón and El Valle, *Duke & Dwyer 13971* (MO, SCZ). Above El Valle, 1000 m, *Gentry 5676* (MO, U). PANAMÁ: 6 mi above Lago Cerro Azul on road to Cerro Jefe, *Croat 15203* (MO). Campo

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[23] *Serjania allenii* Croat, sp. nov. Labrusca fruticosa; corpus lignosum simplex. Folia biternata, viscida infirme; rhachis petiolusque nudus, glandibus elevatis bruneolis infra foliola. Flores cristis brevissimis, emarginatis, squamis villosis secus marginem interioram. Fructus ovatus anguste, circa 3 cm longus, 1.8 cm latus, cordatus inferme ad basim, glaber, viscidus.

Tres beyond Cerro Jefe, ca. 700 m, *Croat 27085* (F, K, MO, PMA, RSA, VEN, US). Cerro Jefe, *D'Arcy 6257* (COL, F, MO, PMA, VEN). El Llano-Cartí Road at km 8–11, 300–400 m, *Mori 7713* (DUKE, MO, PMA).

3. **Serjania atrolineata** Sauv. & Wright, Fl. Cubana 24. 1873. LECTOTYPE: Cuba, *Wright 1587* (BR, G, GH, K, NY, P).—FIG. 12.

S. scatens Radlk., Monogr. Serj. 213. 1875. TYPE: Panama and western Colombia, *Cumming 1132* (K).

S. atrolineata f. *lancifolia* Radlk., Repert. Spec. Nov. Regni Veg. 17: 357. 1921. TYPE: Panama, *Pittier 3379* (NY).

Tendrilled *lianas*, glabrate in age; stems ribbed, minutely appressed-pubescent; wood composite, usually with 3 flattened peripheral bundles, the bundles moderately large, sometimes irregular; sap often drying dark and resinous; tendrils bifid. *Leaves* biternate; petiole, rachis, and petiolule ribbed to narrowly winged; leaflets elliptic to lanceolate to oblanceolate, obtuse to acuminate at the apex, the acumen often blunt with a sharp apiculum, acute to obtuse or attenuate at the base, 4–8.5 cm long, 1.5–3 cm wide, to 15 cm long and 6 cm wide on juvenile leaves, usually dentate above the middle, with distinct, irregular black lines on the lower surface, these sometimes inconspicuous when fresh, the juvenile leaves sometimes with pubescent midribs; stipules minute, ovate. *Thyrses* small, racemose and either solitary in leaf axils or on tendrils, or in open terminal panicles. *Flowers* white, 3–4 mm long; sepals densely tomentose; sepals, petals, and scales with reddish black lines like those of the leaves; petals to 3 mm long, each subtended by a broad green gland, those of the anterior petal with an ear-shaped orange lobe, the scales of the anterior petals ca. 2 mm long, yellow, the crest emarginate, held in front of and slightly below the cluster of stamens, the deflexed appendage densely villous, pendent to almost the base of the petal; stamens 7–9, the filaments pubescent; staminate flowers with the stamens equalling petals, ca. 3 mm long, the pistil very reduced; bisexual flowers with the stamens ca. 2 mm long, the ovary, style and stigma together 3–3.5 mm long, the stigmas 3, ca. 1 mm long, the ovary tomentose. *Fruits* ovate-cordate, 2–2.5 cm long, the cells blackened and densely hirtellous, the wings hirtellous on the inner margin, conspicuously marked with irregular black lines, gradually constricted usually well below the seed-bearing part.

Serjania atrolineata is recognized by the irregular black lines on the leaves, flowers, and fruits. It is one of the more common and widespread species of *Serjania* in Panama.

The species flowers throughout the dry season, January to April, but especially during the latter half of the dry season. Fruits mature in about one month and are mature mostly during March to May.

Serjania atrolineata ranges from Mexico to Venezuela and the West Indies. In Panama it is known principally from drier parts of tropical moist forest but also from tropical dry forest, premontane wet forest, and premontane moist forest.

CANAL ZONE: Barro Colorado Island, *Croat 4673* (F, MO, NY, SCZ), *4941* (MO, SCZ), *7410* (MO), *7685*, *7692* (both F, MO), *7793* (SCZ), *7993* (MO, SCZ), *10304* (MO); *Foster 2164* (DUKE, GH, MICH, PMA); *Shattuck 50* (A, F, MO); *Standley 40963* (US); *Woodworth & Vestal 516* (A, MO), *657* (A, F, MO). Near mouth of Río Chagres, *Allen 886* (F, G,

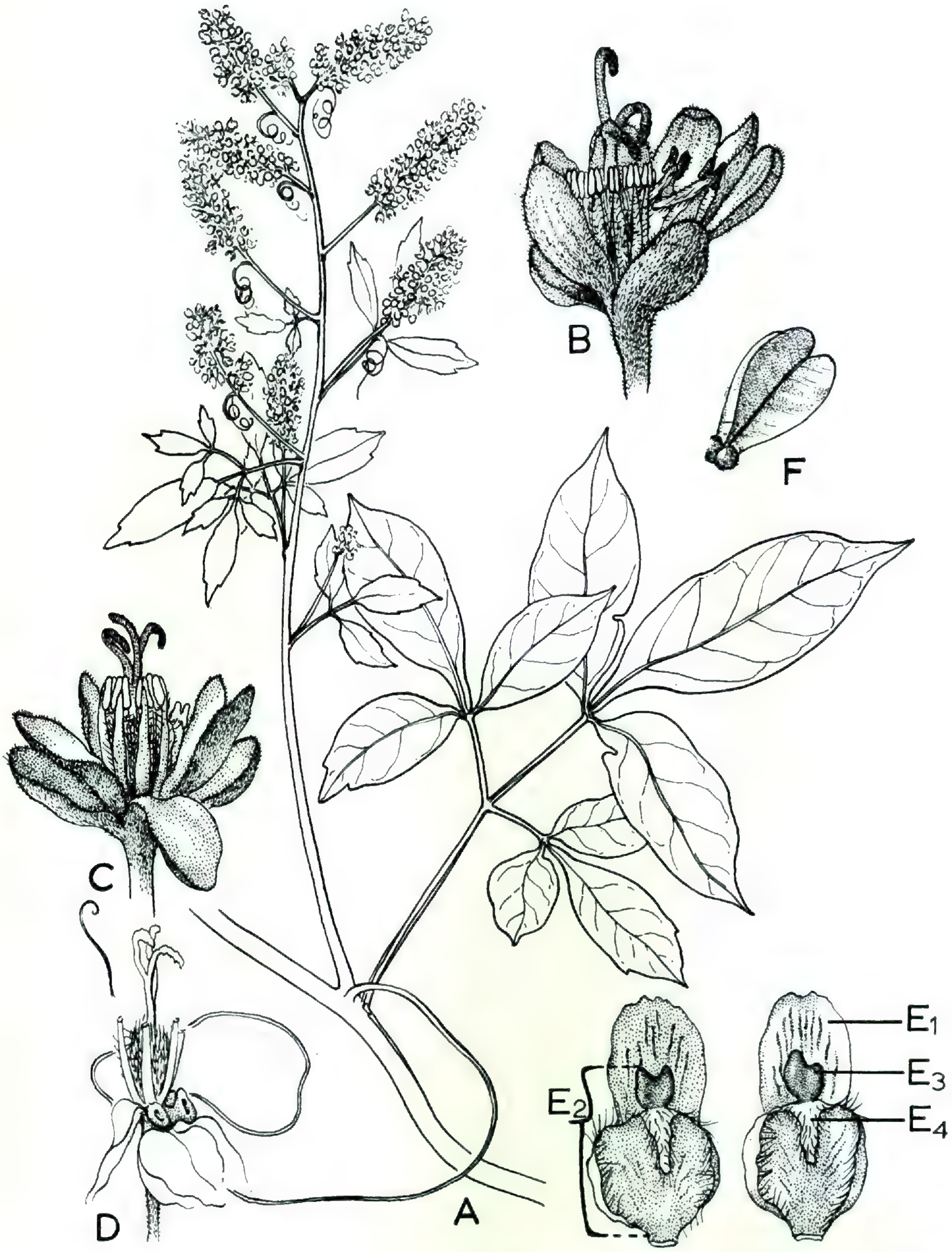

FIGURE 12. *Serjania atrolineata* Sauv. & Wright.—A. Flowering branch (×½). [After *Johnston 1413* (MO).]—B.–C. Bisexual flowers (×6⁹⁄₁₀).—D. Flower dissected to show pistil and disc glands (×6⁹⁄₁₀).—E. Petals with attached scales (×10⅖).—E1. Petal.—E2. Scale.—E3. Crest.—E4. Deflexed appendage. [After *Allen 886* (MO).]—F. Fruit (×⅞). [After *Croat 9153* (MO).]

K, MO, NY, P, US). Victoria Fill near Miraflores Locks, *Allen 1747* (GH, MO). Fort San Lorenzo, *Croat 15438* (MO). Gatún Town, *Hayes 374* (NY, US). Ca. 16 miles N of Gamboa, *Lewis et al. 5442* (MO, SCZ), *5450* (GH, MO), *5451* (MO, SCZ). Boy Scout Road, Madden Dam area, *Maxwell 4022* (DUKE). Río Aqua Salud near Frijoles, *Piper 5871* (US). Vic. of Ancón, *Piper 6033* (C, US). Boy Scout Road, Madden Dam area, *Porter et al. 4022* (MO). Fort San Lorenzo, *Porter et al. 5002* (GH, MO). Miraflores Lake near water plant, *Tyson & Blum 3556* (SCZ). Fort Sherman near point, *Tyson & Blum 3791* (MO, SCZ). CHIRIQUÍ: Burica Peninsula near Punta de Piedra, *Croat 22460* (MO). 4 mi S of Puerto Armuelles, *Liesner 364* (MO). COCLÉ: 1 mi W of Santa Clara, *Tyson 7246* (PMA). Penonomé, 50–1000 ft, *Williams 74* (NY, US). COLÓN: Ridge NE of Trans-isthmian Highway, *Lewis et al. 5411* (GH, K, MO). DARIÉN: Vic. of old gold mine at Caná, SW of Cerro Pirre, *Croat 27303* (MO). Río Pirre, *Croat & Porter 15502, 15545* (both MO). HERRERA: Just S of Ocú, *D'Arcy 4126* (MO), *4128* (GH, MO). LOS SANTOS: 3 mi S of Las Palmas, *D'Arcy 4206* (MO). PANAMÁ: Perlas Isles, Pedro Gonzales Island, *Croat 9153* (MO, SCZ). 2 mi W of El Valle, *Croat 14630* (MO). Isla del Rey, *Duke 9512* (MO). Isla Chepillo, *Duke 10322* (MO). Isla Saboga, *Duke 10347* (MO). Between Río Pacora and Chepo, *Dwyer et al. 5158* (MO, SCZ). San José Island, *Erlanson 26* (GH, US), *180* (GH, NY, US); *Johnston 517* (GH), *663* (MO), *696* (GH, US), *710* (GH), *1413* (GH, MO), *1450* (GH). 16 miles N of Gamboa, *Lewis et al. 5442* (SCZ). Between Sabanas and Río Yugana, *MacBride 2673* (F). Toboquilla Island, *Miller 1985* (US). Sabanas N of Panama City, *Paul 392, 409* (both US). Vic. of Bella Vista, *Piper 5365* (US). Punta Paitilla, *Piper 5396* (US). Between Río Pacora and Chepo, *Porter et al. 5158* (SCZ). SAN BLAS: Vic. of Puerto Obaldía, *Croat 16890, 17008* (MO). VERAGUAS: Trail between Cañazas and the foot of the Cordillera Central, *Allen 200* (A, MO, US). E edge of Cañazas, *Tyson 3731* (MO, SCZ).

4. **Serjania circumvallata** Radlk., Monogr. Serj. 345. 1875. TYPE: Colombia, *Goudot 1* (P).

Glabrous, tendrilled *lianas*; younger stems striate, with milky sap, the older stems grooved, flattened to 3-angled; wood composite, with 3–5(–6?) peripheral bundles, these sometimes obscure, often paired, sometimes flattened. *Leaves* 3-foliolate and pinnate; petioles 2–7 cm long, with marginal ribs above; petiolules short or to 13 mm long; leaflets chartaceous, lanceolate-elliptic, ovate or elliptic, acute to acuminate at the apex, attenuate to rounded at the base, entire to obtusely crenate above the middle, the teeth usually glandular, the terminal leaflet usually 10–14(–19) cm long, 3.5–6.5 (–9) cm wide, the lateral leaflets somewhat smaller, the major lateral veins about 5 pairs, reticulate veins prominulous. *Thyrses* solitary in leaf axils or in terminal paniculate racemes, the ultimate branches densely bracteolate and cincinnal, the branches, pedicels and calyces minutely and densely white-tomentose. *Flowers* white, ca. 3 mm long; sepals oblong to obovate, the 2 opposite the staminal cluster enlarged, obovate, petaloid; petals obovate, glabrous except for villous margins, glandular within near the middle, to 1.7 mm long, all borne on disc glands, the scales of the anterior petals with an obscure, densely villous, deflexed appendage and with a prominent yellow crest deeply 2-lobed to about midway or beyond and extending above the petals, the scales of the lateral petals with a densely villous deflexed appendage, these in contact with the anterior scales; filaments villous to near the apex; ovary minute, glabrous, 3-sided, glandular, the styles 3, equalling the ovary; staminate flowers with the stamens exserted, the longest stamen to 2.3 mm long, all anthers facing anterior petals. *Fruits* ovate, subcordate, 4.5–5 cm long, less than 3.5 cm wide, glabrous, the cells 6–8 mm long and ca. 6 mm wide, rugose, the wings with the veins prominulous, much constricted just below the seed-bearing part.

Serjania circumvallata is distinguished by its glabrous 3-foliolate leaves with thick leaflets bearing a few gland-tipped teeth on the margin.

The species flowers and fruits in the dry season. It ranges from Costa Rica (Golfito) to Colombia. In Panama, it is known from tropical moist forest.

BOCAS DEL TORO: Hill above Milla 7.5 on Almirante-Chanquinola Railroad, *Croat & Porter 16432* (MO, SCZ). CANAL ZONE: Barro Colorado Island, *Croat 12668* (MO). 4 km W of Gatún Dam, 190–200 m, *Nee 8925* (CAS, F, MO, PMA, TEX, US). Barro Colorado Island, *Wetmore & Abbe 195* (A, F, MO); *Woodworth & Vestal 638* (A, F, MO).

5. **Serjania cornigera** Turcz., Bull. Imp. Soc. Naturalistes Moscou. 32: 267. 1859. TYPE: Panama, *Fendler 45* (GH, K, MO, P, W).

Dioecious tendrilled *lianas*, densely rufous-pubescent except sparsely so on the upper surface of the leaflets; stems 5-ribbed; wood simple or composite with at least some of the ribs consisting of separate bundles. *Leaves* biternate; petioles mostly 3–6.5 cm long, ribbed above; rachis margined; leaflets elliptic, blunt to acuminate, abruptly tapered to the base, especially the lateral leaflets, remotely serrate-dentate, the terminal leaflets mostly 7–13 cm long, 3.5–5.5 cm wide, the other leaflets gradually smaller. *Thyrses* paniculate, terminal or in the upper leaf axils, the branches to 15 cm long; pedicels to 1 cm long. *Flowers* white, ca. 7 mm long, unisexual; sepals 5, tomentulose; petals 4, oblong-obovate, ciliolate, the scale of the anterior petals to ⅔ the length of the petal, its crest yellow, thin, emarginate, the appendage villous, slender, pendent to just above glands (scales of lateral petals lacking appendages); rounded disc glands subtending both anterior petals, minutely pubescent on the lower margins, depressed on the outer face, white in staminate flowers, purple at the apex in pistillate flowers; pistillate flowers with stamens to 3.5 mm long, the style 3–4 mm long, the stigmas 3, ca. 1 mm long; staminate flowers with the 5 longer stamens to 6.5 mm long, the shorter ones to 4 mm long, the filaments sparsely villous, the pistil nonfunctional. *Fruits* subrectangular-oblong, ca. 4 cm long, the seed-bearing part rufous-pubescent, subapical, hirtellous and setose with a hornlike projection, the wings scarcely if at all constricted below the seed-bearing part, hirtellous.

Serjania cornigera is characterized by its large flowers, densely rufous-pubescent stems and lower leaflet surfaces, and squarish fruits with the conspicuously setose, seed-bearing parts bearing a hornlike projection.

The species flowers in the earliest part of the dry season in December and January but rarely as early as November. Fruits mature from January to April, mostly in February and March.

The species ranges from Honduras to Panama and it will probably be discovered in Colombia as well. In Panama it is known only from tropical moist forest.

CANAL ZONE: Barro Colorado Island, *Aviles 41* (F, MO); *Brown 118* (F); *Croat 7276* (F, MO, NY), *7410A* (MO), *7424* (MO, RSA, SCZ), *7752* (MO, SCZ), *7823*, *7994*, *12714* (all MO), *12715* (DUKE, F, MO, NY, SCZ), *12797* (MO, SCZ); *Foster 1474* (DUKE, F,

GH, MICH, MO, PMA), *2046* (DUKE, GH, MICH, NY, PMA); *Shattuck 517* (F, MO), *711* (MO); *Wilson 8* (F, MO); *Woodworth & Vestal 330* (A, F, MO). Near mouth of Río Chagres, *Allen 883* (F, G, GH, K, MO, NY, S, U, US). 1.2 mi NW of gate near Gamboa, *Croat 12734* (MO, SCZ). K-6 Road, *Dwyer 3006* (SCZ). Chagres, *Fendler 45* (GH, K, MO, P, W). Margarita, *Gentry 4829* (MO). 2–4 mi N of Gamboa, *Gentry 6534* (MO). Río Providencia, 3 km SE of Achiote, 5–100 m, *Gentry & Nee 8668* (DUKE, MO, PMA). Barbacoas Station, Panama Railroad, *Hayes s.n.* (K). Obispo, *Hayes 136* (GH, NY). 1–3 mi from Gorgona, 40–150 m, *Maxon 4737* (GH, M, NY, US). Between Gatún and Lion Hill, 10–20 m, *Pittier 2568* (M, NY, US). Fort San Lorenzo, *Tyson & Blum 3670* (MO, SCZ). Paraíso, *Wagner s.n.* (M). COLÓN: Between France Field and Cativa1, *Standley 30245* (US). DARIÉN: Río Aretí, *Duke & Nickerson 14915* (MO).

6. **Serjania darcyi** Croat.[24] TYPE: Panama, *D'Arcy & D'Arcy 6401* (MO-2195313, holotype).

Tendrilled *lianas*; stems terete to 6-costate, tomentose; wood simple. *Leaves* biternate; petioles 1–4 cm long, ribbed on the upper surface, glabrous and weakly viscidulous or villous at least on the upper surface; rachis terete to weakly winged; leaflets lanceolate to obovate-elliptic, viscidulous, hirtellous on both surfaces, especially dense on the midrib and veins above, the vein axils of the lower surface sometimes with tufts of trichomes, the midrib prominently raised, the margins subentire to weakly serrate or conspicuously crenate above the middle, the teeth and the tip of the acumen with a conspicuous gland. *Thyrses* narrow, borne on tendrils, 4–15 cm long. *Flowers* white, to 4.5 mm long; pedicels 2–3 mm long, articulate near the middle, the pedicel and calyx tomentose; sepals ovate, glabrate to tomentose within, ca. 3 mm long; petals narrowly obovate, 3 mm long, glabrous, sparsely glandular within, the scales to 2.6 mm long, the basal part rounded, ciliate, weakly villous on the inner surface, the crest orange, thin along the upper margin, rounded, the deflexed appendage ca. 1.3 mm long, only slightly longer than broad, densely and finely white-villous in the lower ⅔; anterior disc glands as broad as long, much thickened at the base, glabrous; staminate flowers with the stamens to 3.5 mm long, the filaments flattened, finely short-villous, the pistil minute. *Fruits* not known.

Serjania darcyi is most easily confused with *S. paniculata*, a species known from Mexico to Colombia and Venezuela and occurring from sea level to 800 m elevation. *Serjania darcyi* differs from that species by having a narrowly winged rachis, more densely pubescent stems, simple wood, and petal scales that are rounded at the apex. It has been found only at 1,800 m elevation.

Flowers are known from August. The species is known only from Panama where it is known from premontane wet forest.

CHIRIQUÍ: Slope of La Popa above Boquete, 5400 ft, *D'Arcy & D'Arcy 6401* (MO).

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[24] *Serjania darcyi* Croat, sp. nov. Labrusca fruticosa cirrhis; rami teretes, 6-costati, tomentosi; corpus lignosum simplex. Folia biternata; petiolus costatus, rhachis teres aut anguste alata; foliola puberula, integra aut serrata leviter aut crenata, dentibus glandulosis manifestis. Thyrsi angusti, 4–15 cm longi, in cirrhis portati. Flores pedicellis calycibusque tomentosis, petalis glabris, cristis squamarum rotundatis. Fructus ignotus.

7. **Serjania decapleuria** Croat.[25] TYPE: Panama, *Croat 7704* (MO-1982638, holotype).

Tendrilled *lianas*; stems weakly 10-costate; wood composite, the large central core surrounded by 10 regular, terete peripheral bundles; branchlets with short crisp pubescence; branchlets, petioles, rachises and petiolules minutely appressed-puberulent; tendrils forked near the apex. *Leaves* biternate; petioles 1.5–8(–13) cm long; rachis without wings; leaflets sessile to short-petiolulate, juveniles often with longer petiolules, oblong-ovate to elliptic, acute to acuminate at the apex, acute to attenuate at the base, entire to dentate with irregular black lines, at least on drying, glabrous except for the usually strigilose midrib and main veins above, the veins axils beneath sometimes with slight tufts of trichomes, the terminal leaflets 6–12 cm long, 2.5–5 cm wide. *Thyrses* in solitary and axillary racemes or in terminal paniculate racemes. *Flowers* white, 4–4.5 mm long; sepals tomentulose; petals narrowly obovate, to 4 mm long, somewhat dark-lineate, the scales of the anterior petals to 3 mm long, the crest emarginate, orange, as broad as or broader than high, the upper margin thin, the deflexed appendages about as long as the crest, densely villous-bearded around its lateral and lower margins; anterior disc glands broader than high, lateral glands about half as broad as the anterior glands; stamens to 3 mm long, the filaments flattened, villous; ovary and styles pubescent, the style 3-branched, the stigma apical. *Fruits* ovate-elliptic, subcordate, subglabrous, 3.5–4 cm long, the seed-bearing part puberulent, 6–7 mm wide, the wings sometimes reddish, subglabrate, weakly constricted just below the seed-bearing part, the veins prominulous.

Serjania decapleuria is most easily confused with *S. insignis* and *S. acuta* in Panama. It is distinguished from both by its composite wood with 10 peripheral bundles. It is distinguished from *S. insignis* also by its larger, densely puberulent fruits, larger flowers, and sparsely pubescent upper midribs. It is further distinguished from *S. acuta* by lacking rufous-tomentose flowers and by having larger fruits.

The species flowers during December and January. Fruits mature from January to March.

Serjania decapleuria is known from Costa Rica to Colombia at elevations between 100 and 700 m. In Costa Rica it is known from San José Province at El General. In Panama it occurs in tropical moist forest in the Canal Zone.

CANAL ZONE: Barro Colorado Island, *Croat 7025* (MO, NY, SCZ), *7704*, *7981* (both MO), *11689* (MO), *12955* (MO, SCZ), *13105*, *14578* (both MO); *Foster 713* (DUKE); *Shattuck 34* (MO); *Wetmore & Woodworth 885* (A); *Wilbur & Weaver 11276* (DUKE). Vic. of Frijoles, *Piper 5792* (US).

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[25] *Serjania decapleuria* Croat, sp. nov. Labrusca fruticosa cirrhis; corpus lignosum compositum centrum magnum fascidibus regularis peripheralis decem circumcinctum. Folia biternata, praeter costam nervosque superne glabra, aliquando caespitosa in axillis nervorum infra foliolam. Thyrsi in racemis solitaribus, axillaribus aut terminalibus paniculatis. Flores 4–4.5 mm longi. Fructus ovatus-ellipticus, 3.5–4 cm longus, subglaber, cellula puberula, 6–7 mm lata, alis rufis.

8. **Serjania grandis** Seem., Bot. Voy. Herald 92. 1853. TYPE: Panama, *Seemann 1643* (K).—FIG. 13.

S. *mollis* Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 345. 1862. TYPE: Peru, between Guerocotillo and Montan, *Bonpland 3670* (P).
S. *cissifolia* Standley, Ann. Missouri Bot. Gard. 27: 317. 1940. TYPE: Panama, *Allen 1021* (F, GH, MICH, MO).

Tendrilled *lianas*, red-tomentose on most parts; stems subterete, with many prominent ribs; wood composite with an irregular number of peripheral bundles, these usually small, paired or solitary, terete or flattened. *Leaves* trifoliolate; petioles 1.5–12 cm long; leaflets ovate to obovate or subrhombic, rounded to obtuse at the apex, rounded to attenuate at the base, 3.5–14 cm long, 2.5–8 cm wide, crenate-dentate, membranous, densely tomentose-pilose especially on the veins. *Inflorescences* axillary thyrses or congested terminal panicles, red-tomentose; bracteoles deltoid, 1.5–3.5 mm long; pedicels ca. 6 mm long, articulate near the middle. *Flowers* ca. 7 mm long; sepals ovate to obovate, short-tomentose, 4–5 mm long; petals broadly obovate-attenuate, 5–6 mm long, glandular inside, the scales of the anterior petals ca. 4 mm long, the crest orange, shortly trilobed or subemarginate, ca. 1 mm long, the deflexed appendage narrowly deltoid, about as long as the crest, glabrous except along the silky long-pubescent margin; bisexual flowers with stamens ca. 2 mm long, the filaments densely silky-white pubescent in the lower half with the trichomes extending to the anthers, the anthers ca. 0.7 mm long, the ovary densely villous, ca. 3 mm long, the style ca. 2.5 mm long, 3-branched to about the middle; staminate flowers not known. *Fruits* ovate-cordate, 2–3.5 cm long, the seed-bearing part trigonous with the apex retuse and the surface villous-tomentose, the wings thin, villous, scarcely or not at all constricted below the seed-bearing part.

Serjania grandis is distinguished by its 3-foliolate, densely red-tomentose leaves, large flowers, and large reddish-pubescent fruits. It is known to flower from November to January and to have mature fruits from December to February.

The species is known from Honduras to Peru. In Panama it occurs in tropical moist forest and premontane wet forest.

CHIRIQUÍ: Vic. of San Félix, 0–120 m, *Pittier 5176* (M, NY, US). Along Río Dupí, near sea level, *Pittier 5434* (M, US). LOS SANTOS: 12 mi S of Macaracas, *Tyson et al. 3080* (MO, SCZ). VERAGUAS: Hills W of Soná, *Allen 1021* (F, GH, MICH, MO). Cañazas, *Tyson 3615* (SCZ).

9. **Serjania insignis** Radlk., Monogr. Serj. 331. 1875. LECTOTYPE: Panama, *Hayes 503* (K).

Tendrilled *lianas*; stems terete with ca. 6 weakly raised ribs, grayish strigose and with a grayish waxy bloom on the epidermis; wood composite, the peripheral

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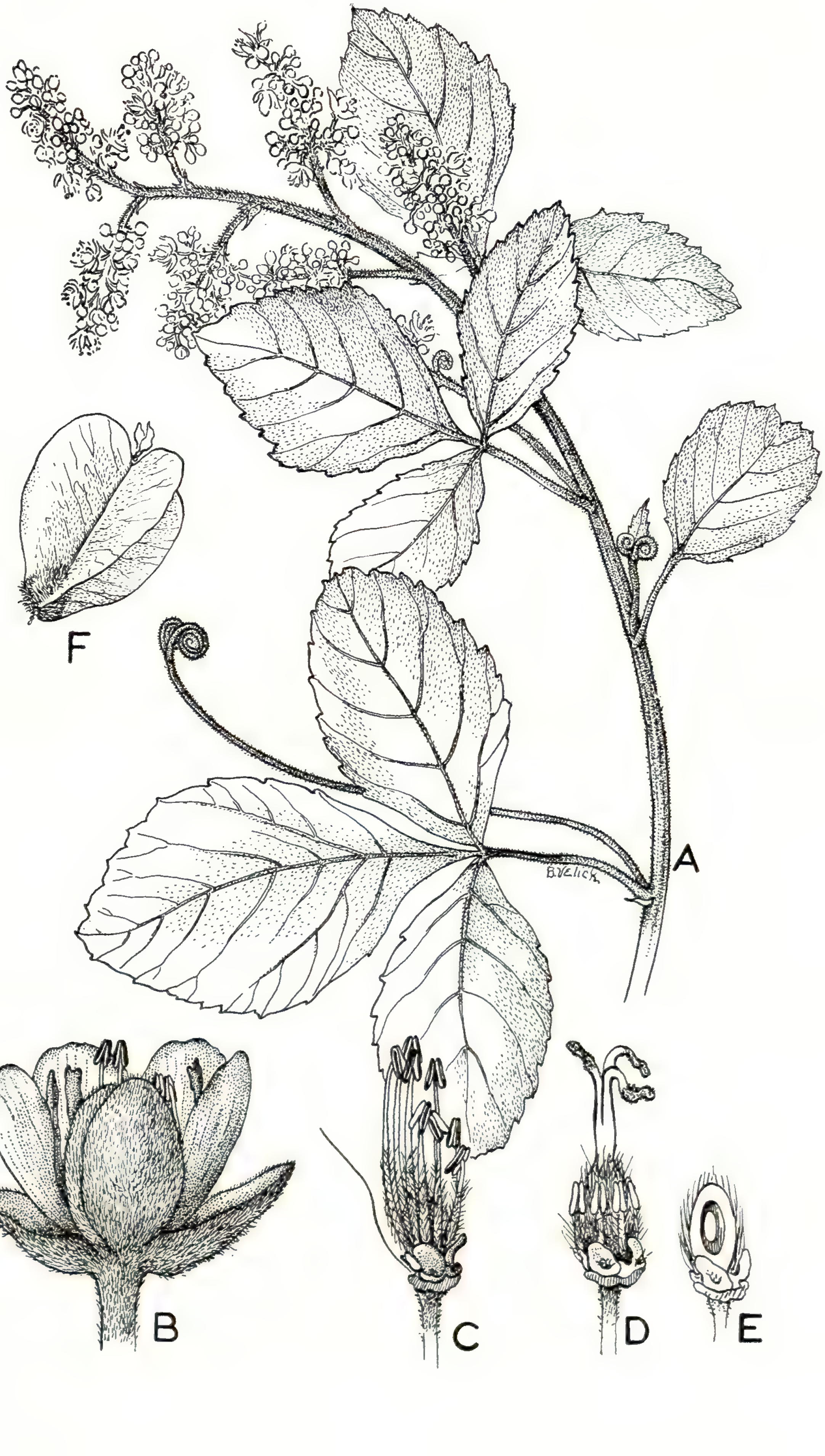
FIGURE 13. *Serjania grandis* Seem.—A. Flowering branch (×7/10).—B. Staminate flower (×57/10).—C. Staminate flower with petals removed (×57/10).—D. Pistillate flower with petals removed (×57/10).—E. Ovary longitudinal section (×57/10). [After *Allen 1021* (MO).]—F. Fruit (×7/10). [After *Tyson et al. 3080* (MO).]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bundles 3 or 4, moderately large, irregular, flattened to terete in larger stems. *Leaves* biternate; petioles terete, 2.5–7 cm long; petiole and rachis without wings; leaflets obovate to oblanceolate, rarely elliptic to subrhombic, acuminate at the apex, acute to attenuate at the base, 4–15 cm long, 2–7 cm wide, subentire to obtusely and remotely crenate in the distal half, glabrate to strigose, especially on the veins and with obscure glandular dots on both surfaces. *Thyrses* solitary in upper leaf axils or on tendrils but usually in a terminal panicle 15–20 cm long, densely strigose, becoming tomentose on the smaller branches and pedicels; bracteoles acute; pedicels 0.5–2.5 mm long, articulate at about the middle, villous to tomentose. *Flowers* white, 2–3 mm long; sepals ovate, strigose to villous, densely ciliate; petals oblong to spatulate, glabrous, ca. 2.5 mm long, glandular within, the scales of the anterior petals shorter than the petals, the crest bifid-emarginate (at least sometimes deflexed); the deflexed appendage densely villous, about as broad as long; filaments villous; ovary 3-sided, glandular, glabrous except on the upper angles. *Fruits* ovate-cordate, 2–3 cm long, as wide as long, constricted slightly at the seed-bearing part, the wings yellowish brown, glabrous, the veins prominulous, the seed-bearing part dark brown, glabrous except for a few trichomes, these usually restricted to the angles, the veins raised.

Serjania insignis has been confused with *S. decapleuria* but is distinguished from that species by having smaller flowers and smaller fruits with a nearly glabrous cell. See also the discussion under *S. decapleuria*. *Pittier 4759*, cited by Radlkofer as *Serjania seemanni* (*S. acuta* Triana & Planch.), is *S. insignis*. Perhaps for this reason Panamanian material of *S. insignis* has long gone by the name *S. seemanni*.

The species flowers in November and December. Fruits mature from December to March.

Serjania insignis is known from Panama and Colombia. In Panama it occurs in disturbed areas in tropical moist forest and also in premontane moist forest.

CANAL ZONE: Along dirt road to Chiva Chiva, *Correa 492* (MO, PMA, SCZ, US). Near Paraíso, *Croat 7157* (MO). Near Summit Garden, *Croat 9073* (MO, SCZ). Gaillard Highway, 2.5 mi NW of Summit Gardens, *Croat 12834* (MO, NY, SCZ). Road E-21, 3 mi from Gaillard Hwy., *Croat 12997* (MO, NY, SCZ). Summit Garden, *Croat 14540* (MO). Ancón Hill, *Croat 15026A* (MO). 3 mi E of Madden Forest, *Croat 15264A* (MO). Between Summit Hills Golf Course and Summit Naval Radio Station, *Croat 16676* (MO). Las Cascades, *Dodge & Hunter 8650* (F, G, GH, K, MO, NY, U, US). Madden Dam, *Dwyer 2097* (MO). Albrook, U.S. ATTC, *Dwyer 7122* (GH, MO, US). Fort Kobbe, *Gentry 2861* (MO). Cerro Galera, *Gentry 6628* (MO). Empire Station, Panama Rail Road, *Hayes 503* (K). Near Paraíso, *Hayes 35* (NY). Paraíso Station, *Hayes 523* (K). Chagres River, ca. 3 mi above Gamboa, *Kennedy et al. 2303* (MO). Empire to Mandinga, *Piper 5496* (US). Boy Scout Road, *Porter et al. 4011, 4020* (both MO). Las Cascadas, *Standley 25718, 29682* (both MO). Cerro Gordo, near Culebra, *Standley 25999* (US). Between Fort Clayton and Corozal, *Standley 29228* (US). 1 mi N of Summit Garden, *Tyson & Blum 1955* (MO, SCZ). Curundú, *Tyson 3479* (MO, SCZ), *Tyson & Blum 2520* (MO, PMA). Chiva Chiva Trail, 1 mi W of Miraflores Lake, *Tyson & Blum 3568* (MO, SCZ). Madden Lake area, *Tyson & Lazor 6152* (MO). 1 mi SW of Cocoli, *Wilbur et al. 12947* (DUKE). Paraíso, *Wagner s.n.* (M). DARIÉN: Río Sabana, ca. 4 mi above Santa Fe, *Duke 10210* (MO). Near Refugio, 15–21 mi N of Santa Fe, ca. 30 m, *Duke 10279* (MO). Río Chucunaque, near sea level, *Gentry 13475* (DUKE, F, MO, NY, PMA, US, VEN). Without exact locality, *Macbride 2690* (F, US). PANAMÁ: Río Maestro, ca. 2 mi from coast, *Gentry 2214* (MO). San José Island, *Johnston 1045* (GH). Bellavista, *Killip 39942* (US). Saboga Island, *Miller 1939* (US). Chepo,

60 m, *Pittier 4759* (GH, M, NY, US). Bellavista, *Standley 25327* (US). Near Punta Paitilla, *Standley 26308* (US, MO). Vic. San Juan Race Track near Panama City, *Standley 27678, 27714* (both US). Near Matías Hernández, *Standley 28943, 32056* (both US). Tumba Muerta Road near Panama City, *Standley 29713* (US). Saboga Island, *Tyson & Loftin 5126* (DUKE, MO, SCZ). WITHOUT EXACT LOCALITY: *Duchassaing 1851* (F, P); *Hayes 326* (NY), *752* (NY).

10. **Serjania mexicana** (L.) Willd., Sp. Pl. 2: 465. 1799.

Paullinia mexicana L., Sp. Pl. 366. 1753. TYPE: Herb. Linn. 512.3 or 513.4 (LINN, not seen, MO, microfiche).
P. caribae Jacq., Obs. Bot. 3: 11, *tab. 62.* 1768. TYPE: *Jacquin* (BM, fragment).
Serjania divaricata (Swartz) Schum., Skr. Naturhist.-Selsk. 3(2): 126, *tab. 12.* 1794, non Griseb., 1861. TYPE: *Swartz* (C, S).
S. *spectabilis* Schum., Skr. Naturhist.-Selsk. 3(2): 126, *tab. 12.* 1794. TYPE: Jamaica (?), *Wright* (BM).
S. *angustifolia* Willd., Sp. Pl. 2: 466. 1799. TYPE: not seen.
S. *pubescens* H.B.K., Nov. Gen. Sp. Pl. 5: 110. 1821, non Seem., 1853. TYPE: not seen.
S. *heterophylla* DC., Prodr. 1: 604. 1824. TYPE: Colombia, Santa Marta, *Bertero* (G, not seen, MO, photo).
S. *samydea* Griseb., Bonplandia 4: 3. 1858. TYPE: *Duchassaing* (GOET, not seen, MO, photo).
S. *nesites* Johnston, Sargentia 8: 185. 1949. TYPE: Panama, *Johnston 707* (GH, holotype; MO, US, isotypes).

Tendrilled *lianas*; trunks to 7 cm diam., involuted, twisted, warty, at least sometimes without milky sap; stems with milky sap, glabrous to villous especially when young, (3–)5-ribbed, the ribs on larger stems in turn 2-ribbed, often sparsely armed with short prickles, especially on larger stems; tendrils bifid, axillary. *Leaves* biternate to 2- or 3-pinnate, 10–40 cm long, often much reduced on the inflorescence, 9–26-foliolate; petioles with marginal ribs above; rachis winged; leaflets ovate to elliptic, obovate or oblanceolate, acute to bluntly acuminate, the acumen often rounded and apiculate, rounded to attenuate at the base, 2–8 cm long, 1.5–5 cm wide, glabrous to sparsely pubescent, especially on the veins, the margin sinuate-dentate near the apex, conspicuously dentate on juveniles, often conspicuously notched on both sides beneath the acumen; stipules deltoid-linear, ca. 5 mm long, to ca. 1 cm long on juveniles. *Thyrses* in solitary racemes in leaf axils, on tendrils, or in terminal or axillary racemose panicles; pedicels slender, 1–3 mm long, densely puberulent. *Flowers* white, sweetly aromatic, 2.5–3.5 mm long; calyx tomentose, the sepals elliptic, to ca. 2.5 mm long, reflexed or spreading at anthesis; petals spatulate to obovate, 2–3.5 mm long, fused at the base with the disc glands, the anterior scales orbicular, nearly ¾ as long as petals, the deflexed appendages slender, glabrous or sparsely pubescent except along their common inner margin, attached laterally to the appendage of neighboring scales by villous pubescence, pendent nearly to the base of scale, the crest yellow, hammer shaped; disc glands 4, large, ovoid, orange, glabrous; filaments flattened, sparsely villous; bisexual flowers with the stamens 1.5–2 mm long, the ovary and style together 2.5–3 mm long, the stigmas ca. 1 mm long, the ovary glandular, sparsely hispidulous medially, the style short, the style and stigmas sparsely hispidulous; staminate flowers with the stamens 2.5–3 mm long, the pistil ca. 0.5 mm long, the ovary 3-sided, glabrous. *Fruits* ovate-cordate, 1.7–2.7 cm long, glabrous, the seed-bearing part with raised veins, the wing usually scarcely if at all constricted below the seed-bearing part.

Serjania mexicana is variable in leaflet number. The species is similar to *S. paucidentata* DC., a species ranging from Mexico to Brazil and Peru, but that species differs in having densely pubescent seed-bearing parts of the fruits.

The species flowers (January) February to April. Fruits mature March to May.

Serjania mexicana ranges from Mexico to Colombia and Venezuela. It is cultivated in Jamaica. In Panama it is known from tropical moist forest and tropical wet forest.

The Spanish common name is "barbasco." Duke (1968) reports it to be used for a fish poison and a toothache remedy!

BOCAS DEL TORO: Río Teribe, *Kirkbride & Duke 475* (MO, NY). Vic. of Chiriquí Lagoon, *von Wedel 2180* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Bartlett & Lasser 16722* (MICH, MO); *Croat 4927* (MO), *5356* (MO, SCZ), *7078* (MO), *8285* (MO, SCZ), *8541* (MO), *9406*, *9552* (both MO, SCZ), *10296*, *12671*, *13263* (all MO), *13814* (DUKE, F, MICH, MO), *13959* (DUKE, F, MO, SCZ), *14026A*, *14065*, *14085*, *14586* (all MO), *14611* (MO, SCZ), *14845A*, *15146A*, *15571*, *16216* (all MO); *Foster 566* (DUKE), *684* (DUKE, F, GH, MO, PMA), *723* (DUKE, F, MICH, MO, PMA), *818*, *1006* (both DUKE, PMA), *1673* (DUKE, MO, PMA); *Shattuck 824* (MO); *Standley 40995* (US); *Wetmore & Woodworth 882* (A); *Woodworth & Vestal 587* (A), *589* (F, MO). Albrook AFB, *Dwyer 6500* (SCZ). Albrook, *Dwyer & Robyns 1* (MO). Chagres, *Fendler 44* (GH, K, MO, US). Gamboa, *Herbierto 80* (US). Pipeline Road, *Kennedy et al. 3058* (MO). Near Miraflores, *White 81* (GH, MO). CHIRIQUÍ: Burica Peninsula, above Quebrada Tuco, *Croat 22104* (MO). Burica Peninsula, near Punta de Piedra, *Croat 22356* (MO). Burica Peninsula, District Quanabano, along Quebrada Quanabano, *Croat 22518A* (MO). Burica Peninsula, District of Barú, along ridge above Brazo Seco near Costa Rican Border, *Croat 22560* (MO). 4 mi S Puerto Armuelles, *Liesner 399* (MO, PMA). Boquete, *Seemann 1211* (K). COCLÉ: NE of Antón, *Croat 9624* (MO). 3 mi NE of Antón, *Croat 9627* (MO, PMA). 8 mi S of El Valle, *Gentry & Dwyer 3573* (MO). Penonomé, 50–100 ft, *Williams 74*, *240* (both NY). COLÓN: Along Río Boquerón near Peluca, *Kennedy 2806* (CAS, MO, PMA). DARIÉN: Near Pidiaque Peak, 800–1000 ft, *Duke 8074* (MO). Manené to mouth of Río Cuasí, *Kirkbride & Bristan 1457* (MO, NY). Marragantí, *Williams 634* (US). HERRERA: Vic. of Ocú, *Stern et al. 1691* (MO), *33567* (MICH, US). LOS SANTOS: Vic. of Tonosí, *Stern et al. 1830* (MO, US), *33653* (MICH, MO). PANAMÁ: San José Island, *Campbell 6* (GH). Cerro Jefe, *Correa 726* (MO, PMA). 10 mi from Pan-Am. Hwy. on road to Cerro Jefe, *Croat 15187* (MO). San José Island, *Erlanson 27* (GH, US), *113* (GH). San José Island, *Johnston 507* (GH), *547* (GH, MO), *550* (GH), *665* (GH, U), *700* (GH, P, US), *701* (GH), *707* (GH, MO, US), *712* (GH, US), *912*, *962* (both GH). Vic. of Panama City, *Macbride 2616* (F, G, GH, US). Bejuco, *Miller 1806* (US). Pacora, *Paul 266* (US). VERAGUAS: 2 mi W of Sante Fe, *Croat 23025* (MO). Between Sante Fe and Escuela Alto Piedras, *Croat 23347* (MO). Cerro Cristóbal, 500 m, *Nee 10143* (CAS, MO, PMA). Without exact locality, *Seemann s.n.* (S). Edge of Cañazas, *Tyson 3736*, *3738* (both MO, SCZ). WITHOUT EXACT LOCALITY: *Cuming 1283* (K); *Duchassaing s.n.* (NY).

11. **Serjania paniculata** H.B.K., Nov. Gen. Sp. Pl. 5: 111. 1821. LECTOTYPE: Venezuela, Prov. Caracasanae near Manterolae, at Tuy River, between San Pedro and La Victoria, *Humboldt & Bonpland 701.711* (P).

Lianas; stems weakly 5-ribbed, viscidulous, tomentulose when young, becoming nearly glabrous on the ribs, weakly to densely pubescent in the sulci; wood composite with a central bundle surrounded by usually 5 smaller bundles. *Leaves* biternate, 8–30 cm long; petioles without wings, 1.8–10 cm long; rachis without wings, with marginal ribs and a medial rib, nearly glabrous except along the upper surface; leaflets elliptic to ovate or obovate, acuminate to obtuse at the apex with a minute apiculum, attenuate and inequilateral or equilateral at

the base, (2–)3.5–11 cm long, (1–)1.8–5 cm wide, crenate to crenate-lobate in the outer half, glabrous on the upper surface except often strigillose on the raised midrib, the lower surface glabrous except for barbulate vein axils and sometimes strigillose veins. *Inflorescences* terminal and paniculate or axillary in the upper leaf axils, the thyrses unbranched, to ca. 12 cm long, viscidulous, tomentulose to villous, angulate; bracteoles deltoid, pubescent; pedicels tomentose, to ca. 2 mm long. *Flowers* white; calyx tomentose on both surfaces; petals oblong-obovate, 4.5–5.5 mm long, glabrous, sparsely glandular on both surfaces, the anterior scales ⅔–¾ as long as the petals, the basal part elliptical, densely villous marginally, the scale deeply bifurcate, 1.1–1.8 mm long, equalling or exceeding the length of deflexed appendage, the lobes narrowly acute, thin, the deflexed appendage deltoid to narrowly triangular, glabrous at the apex, densely villous otherwise; disc glands 4, as broad as or broader than long, glabrous, the anterior ones larger; filaments flattened, villous; staminate flowers with the stamens to 3.5 mm long, the ovary minute, trigonous, glabrous; bisexual flowers with the stamens to 2.5 mm long, the pistil to 4.8 mm long, the ovary oblong-obovate, hispidulous, trigonous, 2 mm long, the style 3-branched from near the middle, glabrous except on the stigmas. *Fruits* narrowly ovate-cordate, 2–2.7 cm long, 1.5–1.9 cm wide, viscidulous, shallowly cordate at the base, weakly constricted below the seed-bearing part, the latter densely whitish-hispidulous, the wings shiny, glabrous except sparsely hispidulous along the inner margin.

The species is easily confused with S. *darcyi*. See that species for a discussion of the differences.

Flowering in Central America occurs in the early dry season from December to February. Fruits mature from February to June.

The species ranges from Mexico to Colombia and Venezuela. It occurs from sea level to 800 m elevation. In Panama it has been collected only on the Burica Peninsula.

CHIRIQUÍ: Guanabano, 2–4 km S of Puerto Armuelles, *Busey 497* (F, MO, PMA, VEN).

12. **Serjania paucidentata** DC., Prodr. 1: 603. 1824. LECTOTYPE: French Guiana, *Martin* (GH).

Paullinia protracta Steud., Flora 27: 725. 1844. TYPE: Surinam (not seen).

Lianas; stems glabrous, 6-ribbed but 3 ribs more prominent, sulcate when young, glabrous; wood composite, usually with 3 small, terete, peripheral bundles. *Leaves* biternate, glabrous, 8–15(–26) cm long; petioles 1.5–4(–8) cm long, canaliculate on upper surface; rachis narrowly winged; leaflets narrowly elliptic to oblanceolate, acute to acuminate and often deeply incised on both sides beneath the acumen, attenuate at the base, 3–13 cm long, 1.8–5 cm wide, thick, mostly entire except for a few crenate, often glandular teeth near the apex, the acumen blunt with a gland-tipped apiculum. *Inflorescences* terminal or usually axillary and borne on tendrils, slender, to ca. 20 cm long; rachis weakly tomentose; pedicels densely tomentose, to ca. 1.5 mm long. *Flowers* white, to 4.5 mm long; sepals ovate to obovate, densely tomentose without, glabrous within, to 2 mm long;

petals narrowly obovate, glabrous, to 4.3 mm long, the anterior scales ca. ¾ as long as petals, stiffly pubescent on margins, the deflexed appendage slender, extending down to about the middle of the scale, densely stiff-pubescent throughout, the crest slightly bilobed, orange, equalling the length of the deflexed appendage; disc glands 2 or 4, semicircular, nearly glabrous; stamens villous, flattened; staminate flowers with the stamens to 4 mm long, the pistil minute, 3-sided, hispid at the apex. *Fruits* narrowly ovate-cordate, weakly constricted below the seed-bearing part, 2.3–2.8 cm long, sparsely hispidulous on the wing, densely brown-hispid on the seed-bearing part.

Serjania paucidentata is closest to *S. mexicana* but can be distinguished by having larger flowers, hispid fruits, unarmed stems, and composite wood.

Flowering occurs from February to April. Fruits are distributed mostly in the dry season but may persist until as late as June.

The species ranges from Mexico to Trinidad, the Guianas, Brazil, and Peru. In Panama it is known from tropical moist forest in the Canal Zone.

CANAL ZONE: Barro Colorado Island, *Croat 7887* (F, MO, NY); *Wilson 83* (F, MO); *Woodworth & Vestal 582* (A, F, MO).

13. **Serjania pluvialiflorens** Croat.[26] TYPE: Panama, *Croat 12421* (MO-2043327, holotype; DUKE, K, MICH, MO, NY, PMA, SCZ, isotypes).

Tendrilled *lianas*; stems terete, the younger stems with a few lines of short, sparse trichomes, otherwise glabrous and vernicose, the older stems glabrous; wood simple. *Leaves* biternate; petiole and rachis angled and slightly ribbed, usually sparsely villous at least on the upper side; petioles 1.5–6 cm long; leaflets ovate to elliptic or obovate, sessile, obtuse to acuminate at the apex, acute at the base, 3–9 cm long, 2–4 cm wide, crenate above the middle, the teeth usually glandular, the surface glandular and pellucid-punctate, glabrous except sometimes short-pubescent on the veins and with axillary villous tufts beneath. *Thyrses* on solitary racemes borne on tendrils and in leaf axils or densely congested in terminal paniculate racemes to 20 cm long; pedicels 1–2 mm long. *Flowers* white, to ca. 4.5 mm long; sepals orbicular to obovate, glabrate to tomentulose outside, pubescent or glabrous within; petals spatulate, to 4.5 mm long, glabrous, the scale ⅔–¾ as long as the petal, each subtended by a triangular to oblong, glabrous gland, the anterior scales ca. 3 mm long, villous especially along the margin, the crest yellow, glabrous, hammer shaped, the appendage densely villous throughout, ca. 1 mm long, the lateral petals with or without subtending glands, their scales lacking crests; disc gland oblong, glabrous; filaments flattened, villous; ovary glabrous or villous near the apex and on the dorsal side of the stigmas. *Fruits* ovate-cordate, glabrous, 2–3 cm long, 1.7–2.3 cm wide, the cell of the fruit

[26] *Serjania pluvialiflorens* Croat, sp. nov. Labrusca fruticosa cirrhis; rami teretes, glabri, vernicosi; corpus lignosum simplex. Folia biternata; petiolus rhachisque fere costatus; foliola sessilia, crenata, pellucida-punctata. Thyrsi in racemis solitaribus in cirrhos aut terminalibus paniculatis. Flores circa 4.5 mm longi; petala glabra, petala antica cristis luteis, petala lateralia squamis sine cristis. Fructus glaber, 2–3 cm longus, 1.7–2.3 cm latus, cellula profunde rugosa. Florescentia tempu pluviali.

deeply rugose with a sharply raised ridge, the wings with prominulous veins, gradually weakly constricted below the seed-bearing part.

Serjania pluvialiflorens is most similar to *S. allenii* but is distinguished from that species by its glabrous, vernicose stems. *Serjania pluvialiflorens* has been confused with *Serjania insignis* Radlk. The latter species is very different both ecologically and morphologically.

Serjania pluvialiflorens is known to flower in September. Fruits mature in October.

The species is known only from Panama in wetter parts of tropical moist forest.

BOCAS DEL TORO: Vic. Chiriquí Lagoon, Fish Creek Hills, *von Wedel 2435* (GH, NY, US). Big Bight, *von Wedel 2888* (MO, US). CANAL ZONE: Barro Colorado Island, in forest north of Zetek Trail 325, *Croat 12421* (DUKE, K, MICH, MO, NY, PMA, SCZ); *Wetmore & Woodworth s.n.* (F).

14. **Serjania rhombea** Radlk., Monogr. Serj. 324. 1875. TYPE: Costa Rica, *Oersted 6683* (C).

S. *paucidentata* Seem., Bot. Voy. Herald 92, no. 142. 1853, non DC., 1857. TYPE: Panama, Darién Prov., Cape Corrientes, *Seemann 599/1* (not seen).

S. *pubescens* Griseb. Bonplandia 6: 3. 1858, non Kunth, 1821, non Seem., 1853. TYPE: Panama, *Duchassaing* (P).

S. *samydea* Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 346. 1862, non Griseb., 1858. TYPE: Panama, Darién Prov., Cape Corrientes, *Seemann 599/1* (not seen).

Paullinia velutina Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 358. 1862. TYPE: Panama, *Fendler 43* (GH, K).

Serjania microcephala Radlk., Smithsonian Misc. Collect. 61(24): 1. 1914. TYPE: Panama, *Williams 31* (NY, US).

Tendrilled *lianas*; stems 6-ribbed, brown-hirtellous, especially on the ribs; wood composite, the peripheral bundles 3, slender, terete, to 4 mm diam. in older stems. *Leaves* biternate, 5–18 cm long; rachis narrowly winged; leaflets ovate to rhomboid, obtuse to acuminate at the apex, obtuse to attenuate at the base, coarsely and obtusely toothed above the middle, shortly pilose, (especially beneath and on the raised midrib above, the terminal leaflet mostly 3–9.5 cm long, 0.5–6 cm wide, the lateral leaflets smaller. *Thyrses* in racemes 5–15(–20) cm long and borne in leaf axils or on tendrils, or in terminal racemose panicles; inflorescence branches softly short-villous; pedicels glabrate, ca. 1 cm long, articulate near the base. *Flowers* white, ca. 3 mm long; sepals ovate, short-tomentose; petals narrowly obovate, ca. 2 mm long, borne atop large greenish glands and subtended by an ear-shaped lobe of the gland, spreading broadly at anthesis, the scales of the anterior petals ca. 1.5 mm long, the deflexed appendage villous, about twice as long as broad, the crest broader than long, bifid, curved away from center of flower; staminal cluster spreading, leaning away from the axis, the filaments sparsely villous, all recurved at the apex; ovary glabrous, the ovary and style together ca. 1 mm long, the style about as long as ovary. *Fruits* cordate-ovate, 1.5–2.2 cm long, about as wide as long, the cell sparsely to densely villous, wings gradually constricted below the seed-bearing part, glabrous or subvillous along the medial sections, often reddish at maturity.

Serjania rhombea is recognized by its rhombic, pilose leaflets, winged leaf rachises, and small fruits with usually reddish wings and densely villous seed-bearing parts. It is perhaps the most abundant species in disturbed forested areas in central Panama. The flowers of the species are unusually small and, unlike most species of *Serjania*, are widely spread at anthesis with the orange appendage crests held to the outside of the flower.

The species flowers principally from November to February. Fruits mature January to May.

The species ranges from Mexico to Colombia, Ecuador, and Venezuela. In Panama it is known from tropical moist forest, premontane moist forest, and premontane wet forest.

CANAL ZONE: Ancón Hill, *Bartlett & Lasser 16323* (MICH, MO). Vic. of Ancón, *Celastine 72* (US). Along road to Chiva Chiva, *Correa 492* (A). Pipeline Road, *Correa et al. 1707* (DUKE, GH, MO, PMA). Near Paraíso, *Croat 7156* (MO). 2 mi NW of Summit Garden, *Croat 9151* (MO). 1 mi NW of Summit Garden, *Croat 12554* (MO). Road C21, *Croat 12982* (DUKE, MO, NY), *Croat 12995* (MO, SCZ). Gaillard Hwy. S of Pedro Miguel, *Croat 13133* (MO). Gaillard Hwy. near Gamboa, *Croat 13143* (MO). 1 mi N of Summit Garden, *Croat 14251* (MO). Near Gamboa, *Croat 14559* (MO). Near Madden Dam, *Dodge 16561* (G, K, MICH, MO, S, U). Ancón Hill, *Duke 4579* (GH, MO, US). Madden Dam, *Dwyer 1951* (MO, US). Chagres, *Fendler 40* (MO), *43* (GH, K). Barro Colorado Island, *Foster 706* (DUKE). Near Summit Hills Golf Course, *Gentry 2821* (MO, U). 3–4 mi N of Gamboa, *Gentry 3352* (MO, TEX). Cerro Galera, *Gentry 6633, 6635* (both MO). 3 mi N of Gamboa, *Gentry & Dwyer 3562* (MO). Balboa Heights, *Greenman & Greenman 5056* (MO). Empire, *Hayes 576* (K). Camino do Corozal, *Herbierto 252* (NY, US). Summit, *Higgins 214* (MO). Along Las Cruces Trail, *Hunter & Allen 689* (F, G, K, MO, U), *739* (G, MO). Between Gamboa and Summit Gardens, *Kennedy 2259* (MO). Near Frijoles, *Killip 3435* (US). ½ mi N of Gamboa, *Lazor & Tyson 5668* (MO). Vic. of Contractor's Hill, *Lewis et al. 2867* (MO). Along K-2 road, *Maxwell 2867* (DUKE). Río Chagres at Gamboa, *Nee 7380* (B, C, CAS, DUKE, GH, L, LE, MEX, MICH, MO, PMA). 6 km ESE of Gamboa, *Nee 8838* (COL, CR, DUKE, GH, MO, PMA, S, TEX, U, VEN). ½ km W of Summit Gardens, 70 m, *Nee 9489* (COL, MO, PMA). Between Rodman Marine Base and Chorrera, *Nowicke et al. 3603* (MO, SCZ). Río Grande near Culebra, 50–100 m, *Pittier 2136* (F, US). K-9 Road, *Smith & Smith 3258* (F, MO, NY, PH). Ancón Hill, *Standley 25161* (US). Balboa, *Standley 25553* (US). Cerro Gordo near Culebra, *Standley 25986* (MO). Near Punta Paitilla, *Standley 26281* (US). Ancón Hill, *Standley 26329* (MO, US). Along Corozal Road near Panama, *Standley 26802* (A, US). Balboa, *Standley 27128* (MO, US). Near Balboa, *Standley 27150* (A, US). Corozal, *Standley 27356, 27366* (both US). Gamboa, *Standley 28454* (US). Between Fort Clayton and Corozal, *Standley 29078, 29216* (both US). Las Cascadas Plantation near Summit, *Standley 29616* (US). Vic. of Summit, *Standley 30098, 30109* (both US). 1 mi N of Summit Gardens, *Tyson & Blum 1977* (MO, SCZ). Barro Colorado Island, *Wetmore & Woodworth 83* (F). Curundú, *Tyson et al. 6078* (MO). Pipeline Road, *Wilbur & Weaver 11214* (DUKE). 1 mi SW of Cocolí, *Wilbur et al. 12857* (DUKE). NW of Gamboa 6 mi, *Wilbur & Teeri 13370* (DUKE). Ancón Hill, 600 ft, *Williams 31* (NY, US); *Woodson et al. 1328* (A, F, MO, NY). COCLÉ: Hills S of El Valle, 600–800 m, *Allen 2865* (F, MO, U). 3 m NE of Antón, *Croat 9610* (MO). 7.5 mi from Penonomé, *McDaniel et al. 14817* (MO). COLÓN: Río Chagres, region above Gamboa, *Allen 4141* (MO). DARIÉN: Near helipad at Hydro Camp on Río Mortí, *Duke 15403* (MO). Outskirts of La Palma, *Gentry 3911* (MO, U). LOS SANTOS: Road from Tonosí to Guanico, *Tyson et al. 3120* (SCZ). PANAMÁ: Pacora vic., 35 m, *Allen 1117* (F, GH, MO, US). Between Capira and Potrero, *Dodge & Hunter 8613* (G, MO, S). Cerro Campana, *Duke 6001* (MO, TEX). Isla del Rey, *Duke 9564* (MO, US). San José Island, *Johnston 1411* (GH). Vic. of Juan Díaz, *Killip 3296* (GH, MO, US). SE slope of Cerro Campana, *Lewis et al. 3097* (MO). Chimán, *Lewis et al. 3341* (MO, PMA). Between Sabanas and Río Yguana, *Macbride 2640* (F, US). 3 km S of Alcalde Díaz (±Cerro Peñón), 410–440 m, *Nee 8574* (CAS, DAV, K, MISSA, MO, P, PMA, VEN). Río Matasnillo, *Osorio 14* (MO, PMA). Sabanas NE of Panama City, *Paul 188* (MICH, US). Laguna

de Portala near Chepo, 50 m, *Pittier 4771* (M, NY, US). Cerro Campana, *Porter 4204* (MO). Vic. of Panamá, *Sargent s.n.* (US). Arraiján Road, *Sharp s.n.* (SCZ). Bellavista, *Standley 25362* (US). Las Sabanas, *Standley 25842* (MO, US), *25922* (US). Río Tapia, *Standley 28176* (US). Río Tocumen, *Standley 29385, 29423* (US). Tumba Vieja near Panamá, *Standley 29740* (US). Juan Díaz, *Standley 30552* (US). Nuevo San Francisco, *Standley 30782* (US). Between Juan Díaz, and Matías Hernández, *Standley 31971, 32000, 32014* (all US). Road to Cerro Campana, *Wilbur & Weaver 11310* (DUKE). SAN BLAS: Mainland opposite Ailigandí *Lewis et al. 72* (GH, MO, US). WITHOUT EXACT LOCALITY: *Duchassaing* (P); *Hayes 148* (GH, US), *285* (NY), *721* (NY), *782* (NY).

15. **Serjania trachygona** Radlk., Monogr. Serj. 327. 1875. LECTOTYPE: Panama, *Seemann 599* (BM, K).

S. *deltoidea* Radlk., Monogr. Serj. 322. TYPE: Peru, Chicoplaya, *Ruiz & Pavon 427* (B, destroyed, MO, photo).

Tendrilled *lianas*; younger stems merely striate or obscurely 3–6-ribbed, the older stems prominently 3-ribbed, each rib consisting of 2 small strands loosely attached to a much larger central core; sap milky; wood composite, usually with 3 pairs of small, terete, peripheral bundles, one of the pairs sometimes united to form a single bundle; tendrils forked; stem, petiole, and rachis puberulous to hirsute. *Leaves* 2–3(–5)-pinnate in 4–6 sets, glabrate to hirsute, especially on the midrib above and on the lower leaflet surface; petioles ribbed; leaf rachis narrowly winged; leaflets small, acute to acuminate, the acumen often rounded and mucronate, acute to attenuate at the base, 1–3.5 cm long, 0.7–2 cm wide, the terminal leaflet rhomboid, often 3-lobed, the lateral leaflets ovate-elliptic, crenate, sessile. *Thyrses* racemose and axillary or in terminal racemose panicles, less than 15 cm long. *Flowers* white, 2–3 mm long, shortly pedicellate; petals ca. 1.7 mm long, obovate, the anterior petals borne on the outer face of large glands, their scales with yellow, prominently bilobed crests, the deflexed appendages densely villous throughout, united as a single unit, pendent to the apex of the glands, the lateral petals borne on top of glands, their crests slender, entire, usually white; staminal cluster leaning away from the center of the flower, the filaments villous; ovary glabrous. *Fruits* ovate-cordate, 1.5–2.1 cm long, as broad as or broader than long, weakly viscid, the seed-bearing part sparsely hirsute with raised veins, the wings glabrous or sparsely hirsute on the inner margin, reddish at maturity, constricted at or just below the base of the cell.

Serjania trachygona is recognized by its usually much compounded leaf with small leaflets and is confused with no other species in Panama. It is variable throughout its range in flower size, leaflet shape, and degree of compounding of the leaves. Juvenile plants have more leaflets than adult plants.

The species flowers in the early dry season from December to February. Fruits mature in the late dry season from February to April.

Serjania trachygona is known from Panama, Peru and Bolivia, but it is probably more widespread in South America. In Panama it is known only from tropical moist forest.

CANAL ZONE: Barro Colorado Island, *Brown 31* (F), *106* (F); *Croat 7810* (MO), *7867* (DUKE, F, MO, SCZ), *7995* (MO), *8218* (MO, SCZ), *8748 12961* (both F, MO, SCZ),

13123, *11472* (both MO, SCZ); *Foster 706* (MO, PMA); *Hladik 52* (MO); *Shattuck 710* (F, MO); *Standley 40904* (US); *Starry 167* (MO); *Wetmore & Woodworth 918* (A); *Wilson 76* (F, MO); *Woodworth & Vestal 521* (A, F, MO). Cerro Galera, 350–400 m, *Gentry 6634* (MO). Gamboa, *Standley 28404* (US). Río Chagres between Río Pequení and Río Indio, 66 m, *Steyermark & Allen 16777* (G, MO). 6 mi N of Gamboa, *Tyson 1505-A* (MO, SCZ). Maune, *Wagner 5981* (M). COLÓN: Near Salamanca, 100 m, *Gentry 6700* (MO). PANAMÁ: Along Juan Díaz River, *Killip 2635* (US). Village of San Juan and Hacienda de San Juan Lamas, *Seemann 599* (BM, K).

14. TALISIA

Talisia Aubl., Hist. Pl. Guiane 1: 349. 1775. TYPE: *T. guianensis* Aubl.

Racaria Aubl., Hist. Pl. Guiane 2: 24. 1775. TYPE: *R. sylvatica* Aubl. = *Talisia sylvatica* (Aubl.) Radlk.

Acladodea Ruiz & Pavon, Fl. Peruv. Chil. Prodr. 133, *tab.* 29. 1794. TYPE: *A. pinnata* Ruiz & Pavon = *Talisia pinnata* (Ruiz & Pavon) Radlk.

Comatoglossum Karst. & Triana in Triana, Nuevos Jeneros Espec. 10. 1854. TYPE: *C. strictum* Karst. & Triana = *Talisia stricta* (Karst. & Triana) Triana & Planch. ex Radlk.

Polygamous, large *shrubs* or *trees*. *Leaves* alternate, pinnate, exstipulate; leaflets opposite or alternate, usually coriaceous, entire. *Panicles* large or small, terminal or subterminal. *Flowers* small, regular; calyx 5-lobed, sometimes to the base, imbricate to nearly valvate, the outer 2 smaller; petals imbricate, unguiculate, villous on the margins, with a scalelike appendage on the inside, at anthesis the petals usually spreading, the scale remaining erect; disc annular or cupulate, fleshy, lobed, pilose; stamens 5–8, borne between the disc and the pistil, sometimes in apparently 2 series, the outer 5 alternating with the petals, the inner 3 reduced, nearest the pistil, the filaments short or elongate, subulate or filiform, glabrous or villous; ovary sessile, villous, ovoid, 3-carpellate, 3-locular, the stigma 3-lobulate, the ovules solitary, ascending from the base. *Fruits* baccate, indehiscent, ovoid or ellipsoid, often 1-celled and 1-seeded by abortion; seed ellipsoid.

This genus of about 40 species is restricted to the American tropics. Five species are known from Panama.

a. Major lateral veins forming a prominent connecting vein before reaching the margin; filaments pubescent.
  b. Most leaves 35–50 cm long; leaflets mostly less than 25 cm long and 5.5 cm wide, often conspicuously bullate; inflorescences 20–30 cm long; calyx more than 2.5 mm wide ..... 2. *T. dwyeri*
  bb. Most leaves more than 100 cm long; leaflets mostly more than 25 cm long and 6.5 cm wide, not conspicuously bullate; inflorescences 30–70 cm long; calyx less than 2.5 mm wide ..... 4. *T. nervosa*

aa. Major lateral veins extending to or almost to the margin, not forming a prominent connecting vein before reaching the margin; filaments glabrous.
  c. Calyx lobed less than halfway, the lobes narrowly triangular, not imbricate at anthesis; disc divided into 5 discrete sections; plants usually branched .... 3. *T. hexaphylla*
  cc. Calyx lobed to the middle or to near the base, the lobes broadly ovate or rounded, imbricate; disc entire, not divided into sections; plants usually not branched.
    d. Calyx 2.5–4 mm long, usually not divided to the base, the lobes usually conspicuously longer than broad; plants bearing conspicuous cataphylls (reduced leaves) in the leaf axils and clustered at the stem apices ..... 5. *T. princeps*
    dd. Calyx less than 2.0 mm long, usually divided to the base, the lobes about as broad as long; plants not bearing conspicuous cataphylls in the leaf axils or near the stem apices ..... 1. *T. allenii*

1. **Talisia allenii** Croat.[27] TYPE: Panama, *Duke 14578* (MO-2198723, holotype; PMA, isotype).

Shrubs or slender *trees* 5–10 m tall, unbranched; stems to ca. 1 cm diam. near the apex, glabrous. *Leaves* to nearly 1 m long, glabrous; petiole 13–17 cm long, prominently enlarged at the base; petiolule pulvinate, 3–8 mm long, canaliculate on the upper surface; leaflets 5–7 pairs, mostly subopposite, narrowly oblong to oblong-oblanceolate, gradually to abruptly acuminate at the apex, acute to attenuate and unequal at the base, 12–33 cm long, 4.5–7 cm wide, often slightly inequilateral throughout their length, the midrib raised on the upper surface, the 10–16 pairs of major lateral veins arcuate-ascending, merging imperceptibly with the margin or forming a weak, irregular connecting vein, the tertiary venation prominulous. *Inflorescences* terminal or subterminal, 40 cm or more long, the longer branches to 20 cm long, the branches and rachis prominently sulcate and sharply angled on drying, puberulent; pedicels to ca. 1 mm long, densely appressed-puberulent, articulate in the upper third. *Flowers* white; calyx bowl shaped, 5-lobed to near the base, 1.5–2 mm long, sparsely appressed-puberulent outside, glabrous within, sometimes somewhat purplish in bud, the lobes broadly ovate, imbricate, much thickened medially; petals narrowly ovate-lanceolate, to 3.8 mm long and 1.6 mm wide, glabrous, white, the scale 3.5–4 mm long, attached to the petal in the lower fourth, densely sericeous inside except in the lower third, sparsely villous to glabrous on the outer surface; disc prominently lobed, ca. 0.6 mm high, glabrous; staminate flower with 5–7 stamens borne between the disc and the pistil, 3 mm long, the filaments glabrous, 2–3 mm long, the anthers oblong, ca. 1 mm long, the ovary pubescent, the style and stigma together ca. 0.6 mm long, pubescent, extending well above the disc; bisexual flowers not seen. *Fruits* narrowly ovoid, 2–2.8 cm long, 1.2–1.8 cm wide, apiculate, minutely muricate on drying and puberulent; seeds oblong, ca. 1.8 cm long and 1 cm wide.

Talisia allenii is most easily confused with *T. princeps* but is distinguished by its much smaller flowers and apparently also by its lack of cataphylls.

The species has been collected in flower during October, January, and February. It is named for Paul Allen who first collected the species.

It occurs in Costa Rica and Panama. In Panama it is known only from tropical moist forest.

DARIÉN: Cerro Yaviza, *Duke & Bristan 431* (SCZ). Without exact locality, *Duke & Bristan 8183* (MO). Río Tuira between Río Punusa and Río Mangle, *Duke 14578* (MO, PMA). WITHOUT EXACT LOCALITY: *Bristan 1511* (MO, SCZ).

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[27] *Talisia allenii* Croat, sp. nov. Arbor parva ad 3.5 mm alta, sine ramis; foliis ad 1 m longis, glabris, foliolis 5–7-jugis, anguste oblongis ad oblongis-lanceolatis, acuminatis, inaequilibus et acutatis ad attenuatis basi, 12–33 cm longis, 4.5–7 cm latis, leviter inaequilateris, nervis lateralis ante marginem non arcuatis confluentibus; inflorescentiis ad 40 cm longis aut longior, ramis manifeste sulcatis, calyce 5-lobo fere usque ad basim, 1.5–2 mm longo, petalis anguste ovatis-lanceolatis, ad 3.8 mm longis et 1.6 mm latis, squama fere longa quam petalo, disco glabro, floribus masculinis staminbus 5–7, portatis inter discum et pistillum, 3 mm longis, filis glabris, floribus femineis ignotis.

2. **Talisia dwyeri** Croat.[28] TYPE: Panama, *Mori & Kallunki 3652* (MO-2245435, holotype; PMA, isotype).

Shrubs 1.3–4 m tall, unbranched; stems glabrous, the leaf scars prominent, ca. 8 mm diam. *Leaves* 35–50 cm long, glabrous; petioles 10–18 cm long, terete, much enlarged at the base; petiolules 3–8 mm long, prominently swollen, flattened on the upper side; leaflets 4–7 pairs, mostly subopposite, narrowly oblong to oblong-lanceolate, gradually acuminate at the apex, acute and slightly inequilateral at the base, 6–25 cm long, 2.5–5 cm wide, becoming conspicuously bullate in age, the midrib prominently raised on the upper surface, the 10–20 pairs of major lateral veins loop-connected by a prominent collecting vein 2–5 mm from the margin. *Inflorescences* terminal or in the upper leaf axils, paniculate, 10–20 cm long, 10–15 cm wide, the longest branches to ca. 10 cm long, the smaller branches, pedicels, and calyces puberulent; pedicels 0.5–1.5 mm long, articulated near the apex. *Flowers* white; calyx deeply bowl shaped, 2.5–3 mm long, 5-lobed ½–¾ to the base, the lobes broadly ovate, imbricate, ciliate, much thickened medially; petals oblong, ca. 5.5 mm long and 2 mm wide, glabrous, the scale fused to the base of the petal for ca. 1 mm, about as long as the petal, glabrous on the outer surface, densely brownish sericeous on the inner surface except at the base; disc prominently 5-lobed, ca. 1 mm high, densely tomentose on the apex; staminate flowers with stamens 5, borne within the disc around the pistil, ca. 5 mm long, the filaments densely villous, slender, ca. 3 mm long, the anthers ca. 2 mm long, oblong-lanceolate, the pistil minute, densely pubescent, the 3 stigmas obscured by the pubescence and extending only slightly above the disc; bisexual flowers not seen. *Fruits* brown, ovoid or ellipsoid, ca. 2.5 cm long, prominently beaked at the apex, weakly appressed-puberulous; mesocarp orange, gelatinous; seed apparently usually 1, ca. 2 cm long, ovoid.

Talisia dwyeri is distinguished by its small inflorescences, small and short leaves, and frequently bullate leaflets. The species is most closely related to *T. nervosa* but is distinguished from that species by its smaller leaves, inflorescences, and calyces.

The species flowers from late November to January. Fruits have been collected in April and July. At least those in July were ripe. The species is named for John Dwyer, the first person to collect the species.

Talisia dwyeri is known only from Cerro Jefe and vicinity.

PANAMÁ: Cerro Jefe, *Croat T-133* (MO); *Dressler 3182* (PMA); *Duke 9448* (MO); *Gentry & Dwyer 3492* (MO). NE of town of Cerro Azul, 20 km by road from Pan-Am. Hwy., *Mori & Kallunki 3652* (MO, PMA). Between Cerro Azul and Cerro Jefe, *Mori et al. 6537* (MO, PMA); *Tyson et al. 4336* (MO, SCZ).

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[28] *Talisia dwyeri* Croat, sp. nov. Arbor parva, 1.3–4 m alta, sine ramis; foliis 35–50 cm longis, foliolis 4–7-jugis, anguste oblongis ad oblongis-oblanceolatis, gradatum acuminatis, acutatis et leviter inaequilateris basi, vetustate bullatis, nervis lateralis ante marginam manifeste arcuatis confluentibus; inflorescentiis 10–20 cm longis, calyce 2.5–3 mm longo, petalis oblongis, ca. 5.5 cm longis et 2 mm latis, floribus masculinis staminibus 5, portatis inter discum et pistillum, 5 mm longis, filis villosis, floribus perfectis ignotis.

3. **Talisia hexaphylla** Vahl, Eclog. Amer. 2: 29. 1798. TYPE: South America, *von Rohr 98* (C).

Talisia panamensis Pittier, Contr. U.S. Natl. Herb. 20: 129. 1918. TYPE: Panama, *Pittier 6534* (US).

Trees or *shrubs* 1–10 m tall (apparently to 30 m in South America), unbranched or usually branched. *Leaves* 25–40 cm or more long; petioles 6–17 cm long, terete, not prominently swollen at the base; petiolule slender, swollen only near the base, 1.2–2.1 cm long; leaflets 5–7, mostly alternate, oblong to oblong-lanceolate, abruptly acuminate at the apex, obliquely cuneate at the base, (4–) 12–21 cm long, (1.2–)4.5–6 cm wide, glabrous except for a minute puberulence on the midrib, the midrib sunken on the upper surface, the major lateral veins mostly 10–12, arcuate ascending or forming an obscure connecting vein, the tertiary venation conspicuous but not prominently raised, the lower surface brownish. *Inflorescences* paniculate, axillary, mostly less than 10 cm long, the branches weakly angulate, spreading, sparsely to densely puberulent; pedicels ca. 1 mm long, articulate at about the middle. *Flowers* white; calyx brown, 3–3.5 mm long, lobed in the upper third, rarely to the middle, densely whitish-tomentose, the lobes triangular, blunt at the apex, the tube narrowly campanulate, appressed-pubescent within except toward the base; petals spatulate to narrowly spatulate, to 5.3 mm long and 1–1.8 mm wide, obtuse at the apex, glabrous on the outer surface above the base, sparsely covered with whitish glandlike trichomes on the outer surface, the scale to 6 mm long, glabrous in the lower third, densely sericeous in upper ⅔ on the inner surface; disc of 5 discrete sections, blackish, ca. 1 mm high, densely villous at the apex; staminate flowers with 8 stamens 3.5–5.5 mm long, the filaments glabrous, the anthers ca. 8 mm long, narrowly elliptic, sometimes with 3 stamens shorter than the others, the pistil minute, shorter than the disc; bisexual flowers not seen. *Fruits* cordate, sessile, ca. 3 cm long, glabrous; seed compressed, ellipsoid, 1.5–2 cm long.

Talisia hexaphylla can be distinguished by its branched stems, shallowly lobed calyx, and discrete lobes of the disc. It is apparently extremely variable in stature. It is similar to *T. congestiflora* Cuatr. from Colombia and may be inseparable from it, but the type of that species has somewhat smaller flowers.

Talisia hexaphylla has been collected in flower during April in Panama. The species is known for certain only from Panama, Bolivia, and in Brazil from the territory of Acre. In Panama it is known only from tropical moist forest and premontane wet forest.

CHIRIQUÍ: Progreso, *Cooper & Slater 170* (US). DARIÉN: Around Pinogana, *Pittier 6534* (US). Marragantí and vic., 10–200 ft, *Williams 1009* (NY).

4. **Talisia nervosa** Radlk., Smithsonian Misc. Collect. 61(24): 4. 1914. TYPE: Panama, *Pittier 4249* (US, fragment at M).—FIG. 14.

Polygamous *shrubs* or small *trees*, usually less than 5 m tall; trunk to 6 cm d.b.h., unbranched (unless damaged). *Leaves* pinnately compound, clustered

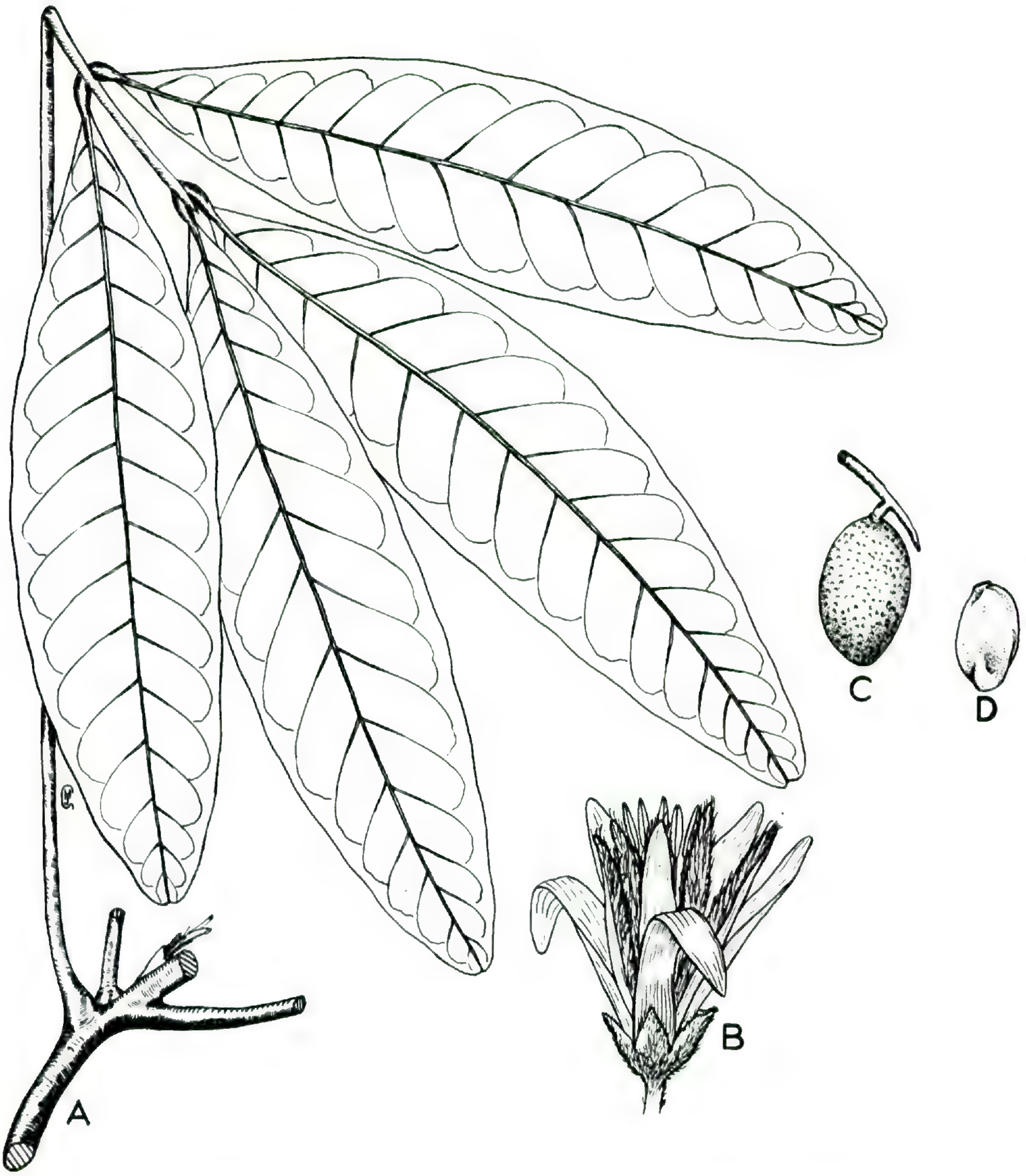

FIGURE 14. *Talisia nervosa* Radlk.—A. Sterile branch (×3/10). [After *Johnston 1778* (MO).]—B. Staminate flower (×5 7/10). [After *Allen* (MO).]—C. Fruit (×3/5).—D. Seed (×3/5). [After *Johnston 1557* (MO).]

near the apex, often 1 m or more long, lacking reduced leaflets at the apex; petioles ca. 25 cm long, terete; petiolules swollen, 5–10 mm long; leaflets usually 5–8 pairs, oblong-elliptic, acute at the apex and base, 20–45 cm long, 6.5–13 cm wide, glabrous above, glabrous to puberulent beneath. *Thyrses* small, arranged in a panicle to 70 cm long, widely branched, the major branches ribbed; branches, pedicels and calyces puberulent to tomentulose; pedicels short, to 2 mm long, articulate below the calyx. *Flowers* white; calyx bowl shaped, to ca. 2 mm long, 5-lobed to about the middle, the lobes indurate, acute, ciliate; petals 5, oblong, 3–5 mm long, acute to blunt at the apex, spreading above the calyx, glabrous, the scale exceeding

the petal, sericeous, tufted and slightly spreading at the apex; disc raised, 5-angulate, the points alternating with the petals; stamens 5 or 8, 3 often reduced or aborted, equalling the scales, to 5 mm long, the filaments weakly pubescent, shorter than the anther, the anthers oblong, 1–4 mm long, the connective beaked at the apex; ovary densely pubescent, those of the staminate flowers less than 2 mm long, the style lacking, the 3 minute stigmas hidden by the pubescence of the ovary; bisexual flowers with the ovary narrowly ovoid, sericeous, the style about as long as the ovary, the stigma capitate, held at about the level of the anthers. *Fruits* ellipsoid to globose, brown, sharply apiculate at the apex, sparsely pubescent, minutely lenticellate, usually 2–3.5 cm long, with a 2–3 mm thick, woody pericarp; seeds ellipsoid, the side flat if more than one, 1.5–2.5 cm long, embedded in a firm or jellylike, whitish to orange mesocarp.

Talisia nervosa is the most common species of *Talisia* in Panama. It is recognized by its large leaflets with prominent connecting veins and by the large inflorescences.

The genus *Talisia* was previously reported to be polygamodioecious, i.e., functionally dioecious but with a few bisexual flowers or flowers of the opposite sex. However, at least some specimens of this species are polygamous, i.e., with large numbers of both bisexual and staminate flowers.

The species flowers in the dry season, December to April, and fruits mature in mid to late rainy season, chiefly July to October.

Talisia nervosa ranges from Costa Rica to Colombia. In Panama it is known from tropical moist forest and tropical wet forest.

Common names include "mamon de monte" (Panama) and "cotupli" (Colombia).

BOCAS DEL TORO: Near Almirante, *Cooper 500* (F, NY). CANAL ZONE: Barro Colorado Island, *Bangham 480* (A, F); *Croat 6498* (F, MO, SCZ), *8095* (MO), *Croat 8236* (F, MO, SCZ), *Croat 8782, 8800, 10873* (all MO), *14027* (MO, SCZ), *14921, 15251* (both MO); *D'Arcy 3916* (MO); *Ebinger 240* (F, MO, US); *Foster 918* (DUKE, PMA), *2210* (GH, DUKE, MO); *Hladik 371* (MO); *Kenoyer 426* (US); *Salvosa 916* (A); *Standley 31421* (US); *Stary 260* MO); *Stimson 5276* (DUKE); *Woodworth & Vestal 631* (A, F, M, MO); *Zetek 4335* (A, F, MO, SCZ, US). Fort Sherman, *Blum & Dwyer 2101* (MO, SCZ); *Dwyer 6940* (MO); *Dwyer & Robyns 140* (MO); *Tyson & Dwyer 1219* (SCZ). Between Fort Sherman and Fort San Lorenzo, *Croat 15415* (MO, NY). Road to Pavon Towers, W of Limón Bay and Gatún Locks, *Johnston 1557* (A, MICH, MO). Maru Towers, NW part of Canal Zone, W of Limón Bay, *Johnston 1712* (A). New part of Canal Zone, *Johnston 1778* (A, MO). Margarita Swamp S of France Field, *Maxon & Valentine 7044* (US). Hills N of Frijoles, *Standley 27575* (US). COLÓN: Santa Rita Ridge, 300–500 m, *Correa & Dressler 629* (DUKE, MO, PMA); *Duke 15250* (MO, SCZ); *Foster & Morton 2245* (DUKE, MO); *Gentry 6603* (MO). Santa Rita Ridge Trail, 400 m, *Mori & Kallunki 6318* (MO). Loma de La Gloria, near Fato, 10–104 m, *Pittier 4249* (M, US). DARIÉN: Summit Camp, between Sasardí and Morí, 400 m, *Duke 10024* (MO). PANAMÁ: El Llano-Cartí Road at km 8–11, 300–400 m, *Mori 7738* (MO). Without exact locality, *Wilbur et al. 11322* (DUKE). VERAGUAS: Isla Coiba, *Dwyer 1548* (MO, SCZ), *2332* (MO, US), *2376* (FLAS); *Foster 1619* (DUKE, GH, MICH, MO, PMA).

5. **Talisia princeps** Oliver, Hooker's Icon. Pl. 18: *tab. 1769.* 1888. TYPE: Venezuela (described from cultivated material at Kew) (not seen).

Polygamodioecious or polygamous *trees* to 6 m tall; trunk slender, to ca. 3 cm wide, prominently ribbed. *Leaves* pinnately compound, to 1 m long or more,

sparsely to densely puberulous except on the blade surfaces; petiolules pulvinate; leaflets 6–14 pairs, opposite or alternate, oblong to oblong-obovate, abruptly acuminate, obtuse to acute at the base, slightly inequilateral, 7–28 cm long, 2.5–6 cm wide, subentire; uppermost leaves (called *Kataphylls* by Uittien) often reduced or aborted, 20–30 cm long, the petiole and rachis flattened, acicular, the leaflets narrowly oblong to linear, brown, dry, achlorophyllous, less than 2 cm long, these reduced leaves having fascicles of still further reduced leaves in their axils in the manner of the adult leaves. *Thyrses* arranged in large terminal panicles to 70 cm long, the lower branches to ca. 40 cm long, the branches ribbed; bracteoles linear-lanceolate, 8–19 mm long; branches, bracteoles, pedicels, and calyces puberulous. *Flowers* white; calyx coriaceous, 2.5–4 mm long, deeply 5-lobed, the lobes ovate, thin and ciliate; petals 5, regular, narrowly obovate, ca. 7 mm long, rounded at the apex, spreading and concave in the upper half, sericeous near the base without, glabrous within, the scale fused to lower third of the petal within, the free part erect, densely white-velutinous, about equalling the petal; disc prominently 5-lobed, the lobes densely villous at the apex; stamens 8, the filaments glabrous (weakly pubescent in Venezuela), longer than the anthers, the anthers ca. 1.5 mm long, the connective beaked at the apex; staminate flowers with stamens 8, ca. 5 mm long, sometimes in 2 obviously differing series, the 5 outer each subtending a large pubescent disc lobe, these alternating with petals, the 3 inner stamens surrounding the pistil, the ovary 0.6–2 mm long, densely sericeous, the trichomes obscuring the 3 triangular stigmatic lobes; bisexual flowers with the stamens ca. 3 mm long, the ovary, style, and stigma together to 6 mm long, the ovary ovoid, 2.5–3 mm long, gradually tapered onto a stout thick style, the style ca. 1.5 mm long, the stigmas 3, short, triangular, usually obscured by the pubescence of the style. *Fruits* glabose, to 4 cm long and 3.8 cm wide, short-apiculate, lightly rugose, 1-seeded (fide Radlkofer).

Talisia princeps is distinguished from other *Talisia* species in Panama by its large flowers and its reduced achlorophyllous or dried upper leaves (cataphylls). Except for the pubescence of the leaves and petals, the species is very close to *T. megaphylla* Sagot from the Guianas and Amazonian Brazil. The inflorescences and flowers are similar to those of *T. bullata* Radlk. from Ecuador but the leaves of that species are poorly known. *Talisia princeps* has other seemingly close relatives in South America including *T. stricta* (Triana & Planch.) Radlk. (Ecuador), *T. cupularis* Radlk. (Brazil), and *T. hemidasya* Radlk. (Surinam).

Talisia princeps flowers in October and November. Time of fruit maturation is not known. Some plants observed in flower on Barro Colorado Island did not set fruit. Possibly the plants are functionally dioecious rather than polygamous as is the general rule in the family.

Talisia princeps is known from Panama and Venezuela. In Panama it has been collected in tropical moist forest and tropical wet forest.

The species is called "sapotero" in Darién (*Gentry 13454*).

BOCAS DEL TORO: Almirante-Changuinola railroad at milla 7.5, *Croat 16376* (MO). CANAL ZONE: Barro Colorado Island, *Croat 8820, 9034, 11270, 12494* (all MO); *Foster 1919* (DUKE, PMA); *Kenoyer 646* (US); *Knight 1020* (MO); *Shattuck 377* (F, MO); *Zetek 3570* (F, MO, US). Between locks at Gatún and Fort Sherman, near sea level, *Croat 15366* (MO). Between

Madden Dam and Saddle II near Alahuela, *Dodge et al. s.n.* (MO). DARIÉN: Cerro Yaviza River near town of Yaviza, *Bristan 431* (US); *Duke & Bristan 431* (DUKE, MO, SCZ). 1–3 km S of El Real, near sea level, *Gentry 13454* (MO, PMA, US). N slopes of Cerro Pirre, 300–700 m, *Mori & Kallunki* 5382 (MO).

15. THINOUIA

Thinouia Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 18: 368. 1862. TYPE: *T. myriantha* Triana & Planch.

Polygamous *lianas* bearing tendrils, these representing sterile peduncles, the branches watchspring-like. *Leaves* petiolate, 3-foliolate; leaflets pinnately veined, usually toothed. *Inflorescences* of thyrses borne on long peduncles, terminal or in the upper leaf axils, usually associated with tendrils. *Flowers* small, yellowish or white, regular or nearly so; calyx short, cupular, 5-parted, the lobes subimbricate; petals 5, spatulate to obovate, bearing scales within at the base; disc small, subcupular, 5-lobed; stamens 8, long-exserted, the filaments villous, the anthers short-ellipsoid; ovary 3-sided, 3-celled. *Fruits* obcordate or cuneate, stipitate, 3-coccus, broadly 3-winged above the seeds, the cocci samaralike, the seed-bearing part basal, the wing large and thin, venose.

The genus has 12 species. Eleven species, including *T. myriantha*, are South American. A single species is known from Central America.

1. **Thinouia myriantha** Triana & Planch., Ann. Sci. Nat. Bot., sér. 4, 369. 1862. TYPE: Colombia, Prov. of Bogotá, Tocaima, Limba, 450 m, *Triana* (BM).—FIG. 15.

T. tomocarpa Standley, Field Mus. Nat. Hist., Bot. Ser. 12: 411. 1936. TYPE: Belize, Temash River, *Schipp 1336* (F, MICH, NY, S, Z).

Lianas; trunks to 12 cm diam., involuted; tendrils watchspring-like; stems terete, minutely appressed ferruginous pubescent and lenticellate, soon glabrous. *Leaves* 3-foliolate; petioles 2–4 cm long; terminal petiolule mostly 2–2.5 cm long, the lateral ones about half as long; blades mostly ovate to ovate-elliptic, acute to acuminate, obtuse to rounded, rarely subcordate at the base, (3.5–)6–12(–15) cm long, (2–)2.5–7(9) cm wide, the midrib arched, the sides folded somewhat upward along the midrib, sparsely pubescent when young, glabrous in age except on the midrib above and in the vein axils of the lower side, 3-veined at the base, the margin undulate, entire or crenate near the apex, the teeth blunt, usually glandular. *Inflorescences* of umbellate thyrses 3–4 cm diam., borne on short axillary or terminal branches to 7 cm long, these often bearing tendrils, the branches, peduncles, pedicles, and calyces appressed-puberulous; pedicels mostly 2.5–3.5 mm long. *Flowers* ±subactinomorphic, minute, greenish; calyx bowl shaped, the lobes 5, uniform, acute, 0.7–1 mm long; petals 5, uniform, obovate, ca. 0.4 mm long, each bearing from the base within a deeply bifid, pubescent scale ca. 1 mm long; disc prominent, ca. 1.1 mm broad, glabrous; stamens 8, actinomorphic, in a tight cluster around the pistil at the center of the flower, 3 erect and held closely together, 5 somewhat divergent, the filaments villous in the lower half, attached to the

FIGURE 15. *Thinouia myriantha* Triana & Planch.—A. Branch with flowers and immature fruits (×½).—B. Fruit (×7/10). [After *Croat 13803* (MO).]

anthers midway, the anthers about as broad as long, the thecae usually separate below the middle; pollen tacky; staminate flowers with the stamens ca. 2.7 mm long, the pistil minute, the styles absent; bisexual flowers with the stamens less than 2 mm long, the pistil stipitate, to 3 mm long, 3-angled, weakly to densely appressed-pubescent, the style short, the stigmas 3, ca. 1 mm long, pubescent, recurved. *Fruits* narrowly ovate-cordate, to 6.5 cm long, brown, glabrous, stipitate, the stipe ca. 5 mm long; samaras to 1.9 mm wide, the seed-bearing part lunate, submarginal, ca. 1.5 cm long, the veins prominulous.

The species is recognized by its terete stems, 3-foliate leaves with basally 3-nerved blades, small, regular flowers in umbelliform clusters, and 3-winged samaroid fruits with basally positioned seeds. There are only a few species of 3-foliolate *Paullinia* and *Serjania*, none of which are vegetatively similar to *Thinouia myriantha*.

Flowering and fruiting occur in the dry season. On Barro Colorado Island, plants observed in flower in February had mature fruits in April and May.

The species is known from Belize, Panama, Colombia, and Venezuela. In Panama it is known from tropical moist forest and tropical wet forest.

CANAL ZONE: Barro Colorado Island, *Croat 13803* (MO); *Foster 2204* (PMA). DARIÉN: La Laguna Ridge between Río Tacarcuna and Río Tapalisa, 400–600 m, *Gentry & Mori 14187* (MO). Around Pinogana, *Pittier s.n.* (US).

16. URVILLEA

Urvillea H.B.K., Nov. Gen. Sp. Pl. 5: 81. 1821. TYPE: *U. ulmacea* H.B.K.

Polygamous *lianas*, usually with axillary tendrils; stems terete or prominently sulcate. *Leaves* stipulate, ternate (Panama) or rarely biternate; leaflets entire to coarsely dentate, sometimes pellucid-punctate, pinnately veined. *Inflorescences* of axillary thyrses, usually associated with tendrils. *Flowers* weakly zygomorphic, small, white; sepals 5, the outer 2 smaller, cup shaped; petals 4, all bearing scales within from the base, these with a broad crest at the apex and a deflexed appendage on the inner side below the crest, the anterior scales better developed than the lateral ones; disc unilateral with 2 or 4 glands; stamens 8, eccentric; ovary sessile, eccentric, 3-celled, the style short, 3-fid; ovules solitary. *Fruits* 3-carpellate; carpels samaroid, seed-bearing in the middle, indehiscent, membranous, broadly winged, separating at maturity from the axis; seeds subglobose, arillate at the base, the testa crustaceous.

The genus has 13 species with only 1 in Mexico, Central America, and Panama.

1. **Urvillea ulmacea** H.B.K., Nov. Gen. Sp. Pl. 5: 82. 1821. TYPE: Venezuela, *Humboldt & Bonpland 629* (P).—FIG. 16.

Vines, the younger parts herbaceous, becoming woody; stems terete when young, striate, sparsely uncinate-pubescent, the older stems terete or 3-sided, 3-sulcate, shiny, glabrate. *Leaves* 3-foliolate, 4–15 mm long; petiole without wings, 1–6 cm long, margined, glabrate to sparsely pubescent; leaflets ovate to

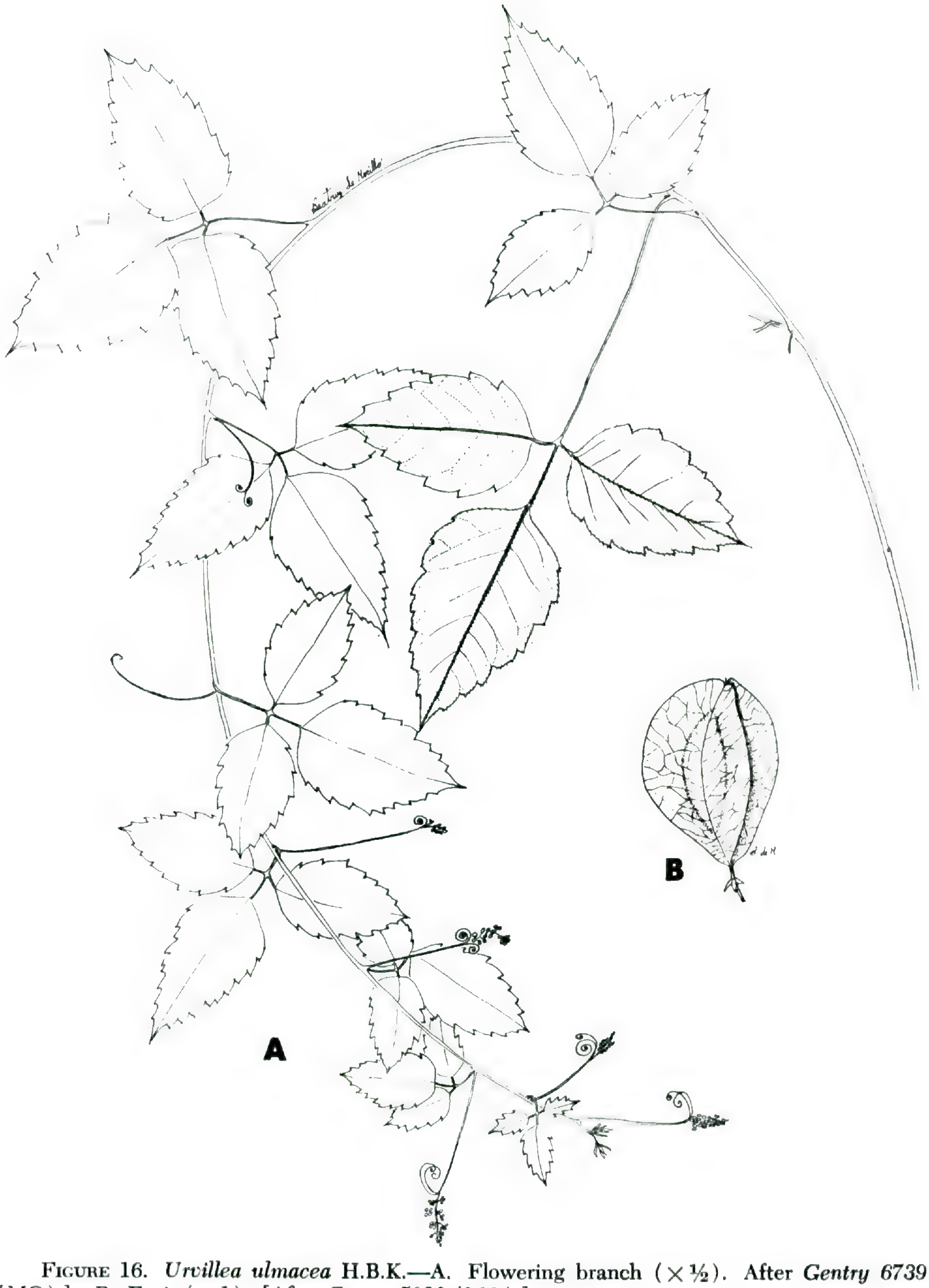

FIGURE 16. *Urvillea ulmacea* H.B.K.—A. Flowering branch (×½). After *Gentry 6739* (MO).]—B. Fruit (×1). [After *Gentry 5032* (MO).]

ovate-lanceolate, acuminate to obtuse at the apex, attenuate at the base on terminal leaflets, obtuse to subcordate on lateral leaflets, 2–7(–9) cm long, 1–3.5(–4.5) cm wide, serrate to crenate marginally except at the base, the teeth glandular, the upper surface strigose to villous on the midrib and some major veins, the re-

mainder glabrous or sparsely puberulent, the lower surface densely pubescent to almost glabrous except on the veins; stipules inconspicuous. *Thyrses* borne on short branches in the upper axils, usually subtended by tendrils, the floriferous part usually less than 3 cm long; pedicels glabrous, 1.5–2.5 mm long, articulate in the lower third. *Flowers* white, to 4 mm long; sepals ovate to ovate-oblong, glabrous, ciliate, the outer sepals to ca. 1.5 mm long; petals obovate, glabrous outside, glandular inside, ciliate, the anterior scales ellipsoid, ½–⅔ as long as the petals, conspicuously ciliate, the crest fan shaped, thin, pale yellow green, conspicuously villous along the upper margin and back side, the deflexed appendage rounded, slightly longer than the crest, glabrous except conspicuously ciliate, the cilia longer than the appendage itself; disc glands 2, large for size of flower, slightly pubescent; stamens free with glabrous filaments; ovary glabrous or minutely puberulent, the style short. *Capsules* elliptic, to 4 cm long and 2 cm wide, obtuse to rounded at the apex, sometimes emarginate, stipitate and acute at the base, the cells somewhat inflated, the wings soft and thin; seeds oval, dark, shiny, 3–4 mm long, the hilum near one end, reniform.

The species is recognized by its small 3-foliolate leaves and inflated, membranous, prominently 3-winged fruits.

Flowering and fruiting may occur throughout much of the year elsewhere but the species is expected to be seasonal in Panama and, like *Serjania*, to flower and fruit in the dry season.

Urvillea ulmacea ranges from southern Texas to Argentina. In Panama it is known from tropical moist forest around Madden Lake and from tropical wet forest in western Panama. It is to be expected elsewhere.

CANAL ZONE: Road between Transisthmian Hwy. and Madden Dam, 100 m, *Gentry 6739* (MO). CHIRIQUÍ: San Bartolo Límite, 300 m, *Busey 422* (F, MO, PMA, US). PANAMÁ: Edge of Madden Lake, *Gentry 5032* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 120. CARYOCARACEAE[2]

GHILLEAN T. PRANCE[3]

Trees, rarely *shrubs* or *subshrubs*. *Stipules* 2–4, usually soon caducous or wanting. *Leaves* petiolate, trifoliolate, opposite or alternate, the margins of the leaflets usually serrate, dentate, crenate or rarely entire, often with stipels at the base of the leaflets. *Inflorescences* of terminal racemes. *Flowers* large, hermaphroditic, actinomorphic; sepals 5(–6), imbricate and large in *Caryocar* or small and reduced in *Anthodiscus*; petals 5(–6), imbricate, caducous, free or rarely slightly connate at the base or connate at the apex to form a calyptra in *Anthodiscus*; stamens very numerous, 55–750 the filaments frequently caducous as a unit together with the petals, usually basally united in a ring, long and slender, and usually with some much shorter interior ones which are often recurved, the apical portion densely tuberculate with minute glandlike tubercles, often with sterile filaments bearing spirally arranged tubercles for their entire length, or an adaxial basal row of sterile staminodes, the anthers basifixed or attached at the middle, bilocular; ovary superior, free, 4(–6)-celled in *Caryocar* and 8–20-celled in *Anthodiscus*, 1 ovule in each locule, the ovules basal, erect, anatropous or atropous; the styles 4 or 8–20, long and slender, apically stigmatic. *Fruits* drupes with the mesocarp indehiscent, usually fatty and fleshy, the endocarp hard and woody, muricate, tuberculate or spinulose on the outer surface, eventually splitting into 1-seeded pyrenes or mericarps; 1–4 seeds developing in *Caryocar*, 8–20 in *Anthodiscus*, often reniform, the endosperm thin or lacking, the embryo with a straight, arcuate or spirally twisted radicle, a fleshy hypocotyl, and 2 small cotyledons. *Pollen* of *Caryocar* subprolate or prolate spherical, tricolporate (very rarely dicolporate or tetracolporate), the exterior reticulate or ornate, 36–120 μ polar diam., 30–114 μ equatorial diam., with characteristic equatorial protusions and prominent apocolpi. The genus *Caryocar* is bat pollinated.

The family contains 2 genera: *Caryocar* with 15 species ranging from Costa Rica to southern Brazil and Paraguay, and *Anthodiscus* with 8 species in Colombia, Venezuela, the Guianas, and northern and western Amazonia. Only *Caryocar* is represented in Panama. *Caryocar* has several species with an edible

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[3] Work carried out while B. A. Krukoff Curator, The New York Botanical Garden, Bronx, New York 10458.

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fruit and also is important as a timber tree. The fruit of at least 3 species is used as a fish poison by Amazonian Indian tribes.

Literature:

Barth, O. M. 1966. Estudos morphológicas dos pólens em Caryocaraceae. Rodriguésia 37: 351–428.

Prance, G. T. 1972. Caryocaraceae. *In* B. Maguire. The Botany of the Guayana Highland IX. Mem. New York Bot. Gard. 23: 127–131.

——— & M. F. da Silva. 1973. Caryocaraceae. Flora Neotropica 12: 1–75.

Vogel, S. 1968. Chiropterophilie in der neotropischen Flora. Flora, Abt. B, 157: 565–569.

1. CARYOCAR

Caryocar[4] L., Mant. Pl. 2: 247. 1771. TYPE: *C. nuciferum* L.

Large *trees* or rarely *shrubs* or *subshrubs*; branches opposite and frequently horizontal. *Leaves* opposite, usually long-petiolate but very rarely almost sessile, trifoliolate; stipules absent or present and soon caducous; leaflets with short petioles, pinnately nerved, the margins serrate, crenate, dentate or rarely entire; often with 2–4 stipels at the base of the leaflets, the stipels persistent or caducous, sometimes with 2 large and 2 small stipels. *Inflorescences* terminal racemes with a short rachis, often corymbose; pedicels apically articulate; bracts seldom developed, usually none, the bracteoles lateral, alternate, small, subpersistent or caducous. *Flowers* hermaphroditic, large; calyx distinctly 5(–6)-lobed, imbricate; petals 5 or rarely 6, imbricate, basally fused together with the base of the filaments and often caducous with the filaments; stamens numerous, 57–750, exceeding the petals, the filaments bent into an S in bud, those on the interior shorter and sterile or with smaller anthers and often a row of short sterile staminodes on the interior, the basal portion of which forms a glandular nectary, the filaments apically tuberculate and the entire length of the smaller filaments sometimes tuberculate, the anthers bilocular, oblong, introrse, dorsifixed or basifixed, longitudinally dehiscent; ovary usually 4(–6)-locular with 1 ovule in each locule, the styles 4, long, filamentous. *Fruits* 4–6-locular drupes with 1–4 locules developing and dehiscing into 1-seeded cocci, the mesocarp thick and fatty or fleshy, the endocarp woody, muricate, tuberculate or spinous on the exterior; seeds reniform or subreniform, the embryo with a straight to arcuate radicle. Germination hypogeal, the first leaves opposite (in 2 species observed).

The genus includes 15 species ranging from Costa Rica to southern Brazil, but it is most abundant in the Guianas and Amazonia. It is predominantly lowland with one species growing on forested uplands in Venezuela.

a. Stipels present; leaf margins coarsely serrate; calyx 6–7 mm long; stamens 150–200; fruit to 6 cm long.

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[4] For a list of synonyms see Prance & da Silva (1973). Only this name has been used for Panamanian material.

b. Leaf underside with a hirsute mass at the junction of the primary veins and midrib; terminal blade 13–16.5 cm long ..... 2. *C. costaricense*
bb. Leaf underside entirely glabrous, without a hirsute mass at the junction of the primary veins and midrib; terminal blade 7–12 cm long ..... 1. *C. amygdaliferum*
aa. Stipels absent; leaf margins entire or weakly crenulate; calyx ca. 20 mm long; stamens ca. 700; fruit to 15 cm long ..... 3. *C. nuciferum*

1. **Caryocar amygdaliferum** Mutis in Cav., Icon. Descr. Pl. 4: 37, *tab. 361, 362.* 1798. TYPE: Colombia, *Mutis 4450* (MA, holotype; F (fragment), NY (fragment), US, isotypes).—FIG. 1.

Trees to 55 m tall; trunk buttressed to 3 m; young branches sparsely puberulous-glabrescent. *Leaves* trifoliolate; petioles 2.5–11 cm long, glabrescent, terete; leaflets shortly petiolulate, the terminal petiolule 4–7 mm long, the lateral petiolules slightly shorter than the terminal one, the petiolules sparsely puberulous, shallowly canaliculate; blades elliptic to oblong, slightly asymmetrical, apically acuminate, the acumen 1–1.5 cm long, basally cuneate to subcuneate and often markedly unequal, the margins unevenly coarsely serrate, glabrous on both surfaces, the terminal leaflet 7.5–12 cm long, 2.5–5.5 cm broad, the lateral blades slightly smaller than the terminal one, the primary veins 10–11 pairs, plane to prominulous beneath, the venation prominulous beneath; stipels to 5 mm long, ellipsoid, inflated, persistent. *Inflorescences* clustered racemes; peduncles 3.5–7 cm long, glabrous; rachis tomentose; pedicels elongate, ebracteolate. *Flowers* with the calyx cupuliform, ca. 6 mm long, glabrous on the exterior, the lobes 5, small, rounded, the margins ciliate; corolla lobes 5, ca. 2–2.5 cm long, oblong, glabrous, greenish yellow; stamens numerous, ca. 200, the filaments basally shortly united in a ring, but into groups, white, sparsely pubescent, the apical portion tuberculate, the innermost filaments much shorter than the rest, the anthers small; ovary globose, glabrous on the exterior, 4-locular; the styles 4, filamentous, shorter than the filaments. *Fruits* globose-ellipsoid, ca. 5.5 cm long, the exocarp glabrous, smooth, the pericarp thick, fleshy, the mesocarp and endocarp enveloping the seed to form an ovoid stone, the exterior of the mesocarp not seen, the interior enveloping the endocarp tubercles, the endocarp with numerous flattened tubercles ca. 5 mm long, and a hard woody interior ca. 1 mm thick, glabrous within.

This species is also common in the Magdalena valley region of Colombia. It is most closely related to *C. costaricense* from which it differs in the absence of a hirsute mass at the junction of the primary veins and petioles, the smaller leaves with a more coarsely serrate margin, and the more inflated stipels.

The fruit of this species is used as a fish poison in Colombia, and the wood is used as a commercial timber.

DARIÉN: Punta Guayabo Chiquita, 14 mi N of Colombia, *Stern & Chambers 161* (MO).

2. **Caryocar costaricense** Donnell Smith, Bot. Gaz. (Crawfordsville) 55: 431. 1913. TYPE: Costa Rica, *Pittier 12115* (F, US).

Trees to 50 m tall; trunk buttressed to 1.5 m; young branches sparsely puberulous-glabrescent. *Leaves* trifoliolate; petioles 4.5–12.0 cm long, sparsely puberu-

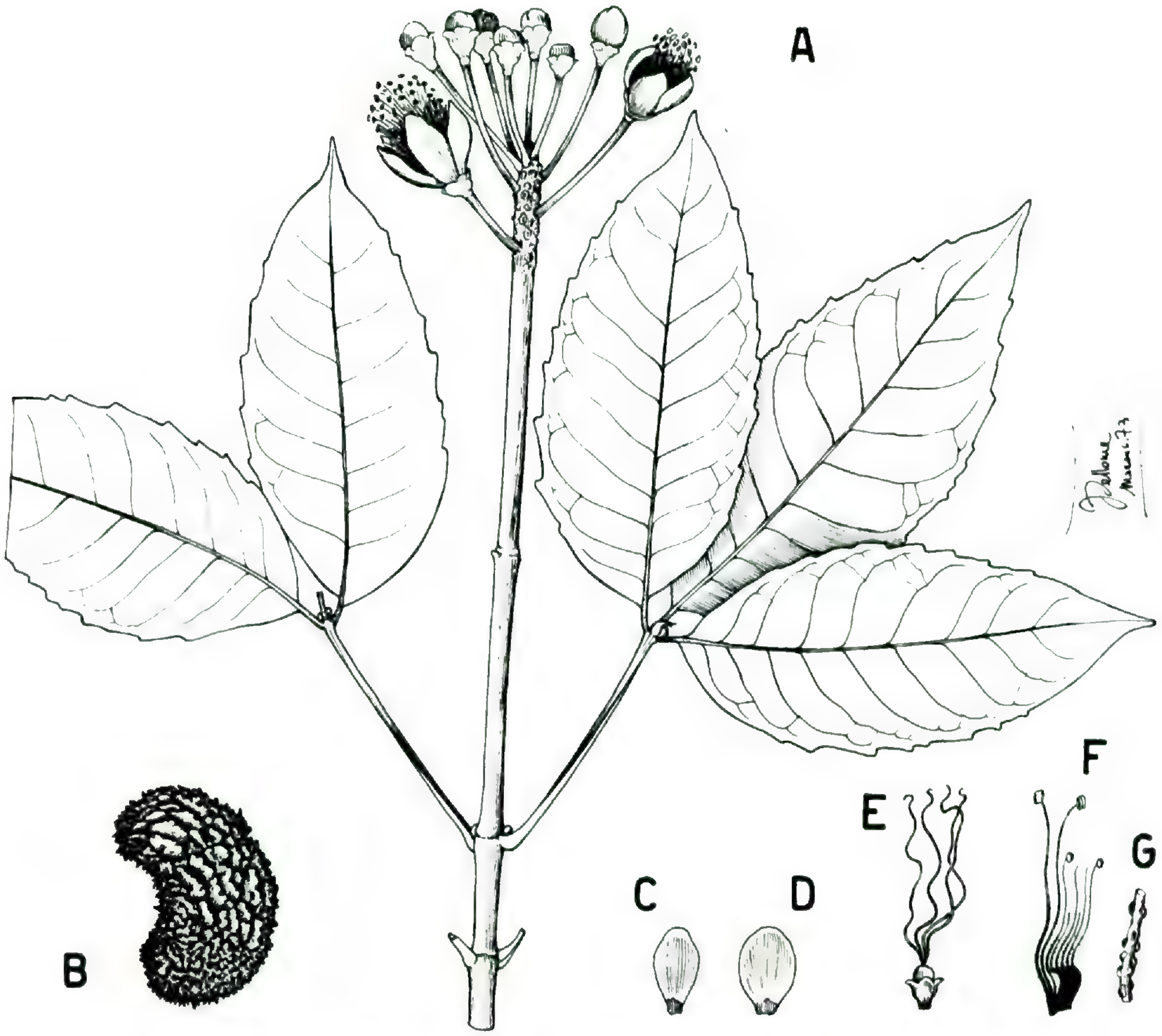

Figure 1. *Caryocar amygdaliferum* Mutis.—A. Habit (×½).—B. Endocarp of fruit (×½).—C–D. Petals (×½).—E. Ovary and styles (×½).—F. Arrangement of stamens (×½).—G. Tubercles on filaments (×½). [After *Romero C. 4840* (COL), Colombia.]

lous-glabrescent, terete; leaflets shortly petiolulate, the terminal petiolule 2.0–3.0 mm long, the lateral petiolules sparsely puberulous-glabrescent, terete; blades oblong, apically slightly asymmetrical, acuminate, the acumen 10.0–15.0 mm long, basally rounded to subcuneate and unequal, the margins serrate, glabrous above, glabrous beneath except for hirsute masses in the axils of the primary veins, the terminal blade 13.0–16.5 cm long, 6.0–7.5 cm broad, the lateral blades slightly smaller than the terminal one, the primary veins 10–12 pairs, plane or shallowly impressed above, prominent beneath, the venation plane to prominulous beneath; stipels persistent, to 1.0 cm long, inflated. *Inflorescences* clustered racemes, ca. 30–35-flowered; peduncles 9.0–15.0 cm long, sparsely puberulous-glabrescent, terete; rachis 2.0–3.5 mm long, sparsely puberulous; bracteoles 2, caducous. *Flowers* with the calyx cupuliform, 6.0–7.0 cm long, sparsely puberulous on the exterior, the lobes 5, ciliate, rounded; corolla 2.0–2.8 cm long, the lobes 5, oblong, glabrous, yellow; stamens numerous, ca. 150, the filaments basally shortly united but not into groups, 4.0–5.0 cm long, yellow, tuberculate towards the apex, the

anthers small; ovary globose, 4-locular, glabrous on the exterior, the styles 3–4, filamentous, glabrous, ca. 2.0 cm long. *Fruits* not seen.

SAN BLAS: Mountains above Puerto Obaldía, *Gentry 1482* (MO).

3. **Caryocar nuciferum** L., Mant. Pl. 2: 247. 1771. TYPE: Guyana, *Allemand* (not seen).

Pekea tuberculosa Aubl., Hist. Pl. Guiane 1: 537. 1775, pro parte quoad fruct. tantum.
Rhizobolus tuberculosus (Aubl.) Gmel. in L., Syst. Nat., ed. 13, 2(1): 840. 1789, pro parte.
R. pekea Gaertn., Fruct. Sem. Pl. 2: 92, *tab.* 98. 1790, pro parte, nom. illeg.
Caryocar tomentosum Willd., Sp. Pl., ed. 4, 2: 1244. 1799, pro parte, nom. illeg.
Amagdala guayanensis Clusius, Exoticorum 27, *tab. 1.* 1605, nom. illeg.

Large *trees* to 45 m tall; young branches glabrous. *Leaves* trifoliolate; petioles 4–20 cm long, terete to flattened, glabrous; leaflets petiolulate, the terminal petiolule 7–25 mm long, the lateral petiolules about equal to the center one, the petiolules glabrous, terete or shallowly canaliculate; blades elliptic, apically acuminate, the acumen 5–15 mm long, the margins entire to weakly crenate, basally rounded to subcuneate, glabrous on both surfaces, the terminal blade 12–34 cm long, 6–18 cm broad, the lateral blades equal or slightly smaller than the terminal one, the primary veins 8–18 pairs, plane above, prominent beneath, the venation prominulous beneath; stipels absent. *Inflorescences* clustered racemes; peduncles 6–10 cm long, glabrous, sparsely lenticellate towards the base; rachis 1–4.5 cm long, glabrous; flowering pedicels 4–6 cm long, 5–8 cm thick, glabrous, ebracteolate. *Flowers* with the calyx campanulate, ca. 2 cm long, glabrous on the exterior, the lobes 5, rounded; corolla ca. 6–7 cm long, elliptic, glabrous, deep red on the exterior, paler within; stamens extremely numerous, over 700, the filaments caducous as a unit, basally united to 2 mm and then dividing into fused groups before becoming free above, the outer ones 7–8.5 cm long including the base, yellow, the distal portion tuberculate, many shorter inner filaments present from 3.5 cm long and of all intermediate sizes, the inner filaments only apically tuberculate, the anthers small; ovary globose, 4-locular, glabrous on the exterior, the styles 4, filamentous, 8–9 cm long, glabrous. *Fruits* subglobose to sublobate, to 15 cm long, the exocarp glabrous, lenticellate, the pericarp very thick and fleshy, detaching from the mesocarp and endocarp, the mesocarp and endocarp enveloping the seed to form a large stone ca. 7 cm broad, 5 cm long, the mesocarp becoming lignified and hard, the exterior undulate with short rounded tubercles, the endocarp with a tuberculate exterior and a hard thin woody interior ca. 1 mm thick; only 1–2 subreniform seeds developing.

The material cited below is sterile and is with some hesitation assigned to *C. nuciferum*, a species otherwise confined to the Guianas. Only fertile material will show whether this is the same species. However, similar distribution patterns between the Guianas and the uplands of Panama occur in other groups. The leaves and the young stem are a good match with *C. nuciferum*.

C. nuciferum is grown in the Guianas and Caribbean where the edible fruit is sold in the markets as the Souari nut.

DARIÉN: Extreme summit of Cerro Pirre, 1000–1400 m, *Gentry 7023* (MO, NY).

INDEX OF LATIN NAMES

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 157. SYMPLOCACEAE

W. G. D'ARCY[2]

Trees or *shrubs*; pubescence of simple hairs, sometimes multicellular and sclerified with inconspicuous septations; twigs pubescent. *Leaves* alternate, entire or serrate, both sometimes on the same plant, mostly elliptic, mostly glabrous and often shiny above, glabrous or pubescent beneath, often coriaceous, often yellowish green, pinnately veined and the midvein impressed above, elevated in the lower half beneath, vernation involute; petioles short; stipules wanting. *Inflorescences* axillary, mostly short racemes or spikes, sometimes fascicled, short panicles, or solitary flowers; bracts small, often caducous; pedicels present or wanting, often subtended by or bearing bractlets, these sometimes forming an involucre of 1–3 elements. *Flowers* perfect (Panama) or rarely androdioecious, small; calyx united halfway, the 4–9 sepals imbricate, mostly rounded, often ciliate; corolla sympetalous, divided halfway or nearly to the base into 3–11 imbricate petals in 1–2 whorls; stamens 5–100, the filaments basally fused into a short column which is adnate to the corolla tube or petals, the filaments becoming thicker and straplike above the column, separating in clusters or singly or remaining fused to high levels, apically contracted into a filiform stipe, the anthers small, rotund, 2-locular, basifixed, versatile; ovary 2–6 locular with 2–4 anatropous, pendant, epitropous ovules in each locule attached to axile placentas, half or more inferior, the superior portion often cylindrical, flat topped (Panama) glabrous, tomentose, or with a glandular covering, the style single, slender, broader at the base, sometimes furrowed, glabrous or basally pubescent, sometimes minutely muricate, the stigma capitate, often demarcated into several small, irregular lobes. *Fruits* stony drupes surmounted by the calyx lobes, glabrous or pubescent, blue, yellow, brown, or black, mostly elliptical but sometimes obovoid or slightly curved, with 2–6 locules, abortive locules sometimes fusing to form larger cavities and usually 1 seed maturing in each cavity; seed ellipsoidal, sometimes slightly bent, the embryo straight or slightly curved, endosperm abundant. *Pollen* 3-colporate.

The literature contains conflicting reports about the septation of the upper portion of the ovary and the placentation in this region. Brand (1901) stressed the fundamental 5-merous condition of the flowers, but the number of parts varies considerably, and as the staminal column is adnate to only the inner petals, the

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[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

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perianth may be considered cyclical. It is also not certain whether the stamens are fundamentally alternate with or undetermined with respect to the petals.

Chromosome counts of $n = 11$ and $n = 12$ appear in the literature for several species (not Panamanian).

Species of Symplocaceae are well known as accumulators of aluminum which correlates with yellowish green leaf color and blue fruits (Chenery 1948–1949). The foliage of some species is sweet to the taste and is relished by livestock. Some species have been used to make yellow dyes.

The family is usually considered to comprise one genus with some 300 species but some workers recognize a section of Indonesian species as the segregate genus *Cordyloblaste*. Symplocaceae was long considered closely related to the Styracaceae and included in it by some botanists, but more recent workers have allied it with the Theaceae.

Literature:

Brand, A. 1901. Symplocaceae. *In* A. Engler (editor), Das Pflanzenreich. IV. 242 (Heft 6).

Chenery, E. M. 1948–1949. Aluminum in the plant world. Kew Bull. 3: 173–183; 4: 462–473.

1. SYMPLOCOS

Symplocos[3] Jacq., Enum. Pl. Carib. 5. 1760. TYPE: *S. martinicensis* Jacq.

Shrubs or *trees*; twigs pubescent. *Leaves* alternate, entire or serrate, sometimes on the same plant, mostly elliptic, glabrous, shiny above, coriaceous; petioles short; stipules wanting. *Inflorescences* axillary, short, many–1-flowered; bracts small; pedicels present or wanting; bractlets often present. *Flowers* perfect (Panama), small; calyx with sepals 4–9 united halfway, imbricate, often ciliate; corolla sympetalous, divided halfway or more into 3–11 imbricate petals in 1–2 whorls; stamens 5–100, the filaments fused into a short basal column which is adnate to the corolla, the anthers small, rotund; ovary 2–6 locular, flat topped, half or more inferior, 2–4 pendant ovules in each locule, the style single, short, the stigma capitate. *Fruits* stony drupes surmounted by the calyx lobes.

In the most recent monograph, Brand (1901) considered *Symplocos* to comprise nearly 300 species in 4 subgenera and 8 sections. The Panamanian species all belong to subsect. *Ciponimastrum* of sect. *Symplocastrum* which includes some 70 species of the New World tropics. Brand placed this section and sect. *Cordyloblaste* of Indonesia together in subgenus *Symplocos* (*Eusymplocos*).

a. Leaves manifestly pubescent beneath, mostly more than 8 cm long; calyx densely pubescent; fruit puberulent.
   b. Leaves more than 5 cm wide; corolla more than 10 mm long; petals tomentose outside ..... 3. *S. serrulata*
   bb. Leaves less than 5 cm wide; corolla less than 10 mm long; petals mostly glabrous except for hairs near the apex and along the costa ..... 1. *S. austin-smithii*

aa. Leaves glabrate beneath, mostly less than 8 cm long; calyx ciliate but otherwise glabrate; fruit glabrous ..... 2. *S. chiriquensis*

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[3] For synonyms see Brand (1901). Only this name has been used for Panamanian material.

1. **Symplocos austin-smithii** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 915. 1938. TYPE: Costa Rica, *Austin Smith A380* (F, holotype; MO, isotype).

S. *brenesii* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 916. 1938. TYPE: Costa Rica, *Brenes 4456* (F, holotype).

Trees to 20 m tall, slash red; twigs canescent with mostly ascending, mostly appressed, long, stout, uniseriate hairs. *Leaves* 4–12 cm long, 25 cm wide, elliptical or obovate, apically acuminate with a short drip tip, basally obtuse, the margins entire or crenulate, chartaceous, glabrous and drying dark above, lighter beneath and softly pubescent with long, dispersed, mostly straight, appressed hairs; petiole ca. 10 mm long, canaliculate above. *Inflorescences* short, axillary racemes or panicles; peduncle short, to ca. 8 mm long, stout, densely reddish or yellowish tomentose; bracts caducous; pedicels short or wanting. *Flowers* white; calyx densely canescent outside, the sepals obtuse or rounded, ca. 2 mm wide, 2½ mm long, glabrous near the margin but ciliate at the margin; corolla 7–8 mm long, the petals free except almost at the base, pubescent outside, sometimes only near the tips; stamens numerous; style long-pilose near the base, the ovary densely pilose. *Fruits* ellipsoid, 20 mm long, 10–12 mm across, the apical, superior portion of the ovary 5–6 mm across, 3-locular.

CHIRIQUÍ: Boquete, 500 ft, *Davidson 803* (MO, US). Volcán de Chiriquí, Boquete, 7000 ft, *Davidson 887* (US). Cerro Horqueta, 1500 m, *Duke et al. 13614* (MO, PMA). Cerro Punta, 2000 m, *Lao 346* (MO). Finca Collins, 5800–6700 ft, *Stern et al. 2028* (MO, US). Valley of upper Río Chiriquí Viejo, *White 339* (F, MO).

2. **Symplocos chiriquensis** Pittier, Contr. U.S. Natl. Herb. 18: 168. 1916. TYPE: Panama, *Pittier 2994* (US, holotype; NY, isotype).—FIG. 1A–B.

Shrubs or *trees* to 30 m tall; twigs appressed canescent, soon glabrescent, light colored, terete or slightly furrowed. *Leaves* clustered near the ends of twigs, elliptical or obovate, 5–7 cm long, 2–3 cm wide, apically blunt-acuminate, basally narrowed, the margin entire, crenate or serrate, coriaceous, often drying with a yellowish cast, the lateral venation often obscure; petioles 5–10 mm long. *Inflorescences* short-racemose, sometimes appearing fascicled; peduncles tomentose to glabrate; bracts tomentose, ciliate, caducous; pedicels short or wanting, glabrate. *Flowers* 6–8 mm long, fragrant, white or pinkish; sepals rotund, 3 mm wide, 2 mm long, ciliate, otherwise glabrate, conspicuously thinner at the margins; petals 5–6, 7 mm long, apically cuculate, the bottom 1 mm connate, the free portion basally ciliolate, otherwise glabrous; stamens ca. 25, the filaments separating in groups of 3–12 at various heights, the apical stipe 0.3 mm long, the anthers rotund, ca. 0.4 mm across; ovary ca. 2 mm across, the free, cylindrical portion ca. 0.6 mm tall, truncate, tomentose, the style glabrous (slightly hairy at the base according to Pittier), the stigma an irregular, capitate mass. *Fruits* ellipsoidal, ca. 15 mm long, 8 mm across, grayish, 4-locular.

This species occurs in central and western Panama and in Costa Rica where it has been confused with S. *costaricana* Hemsley, a species with a glabrous ovary.

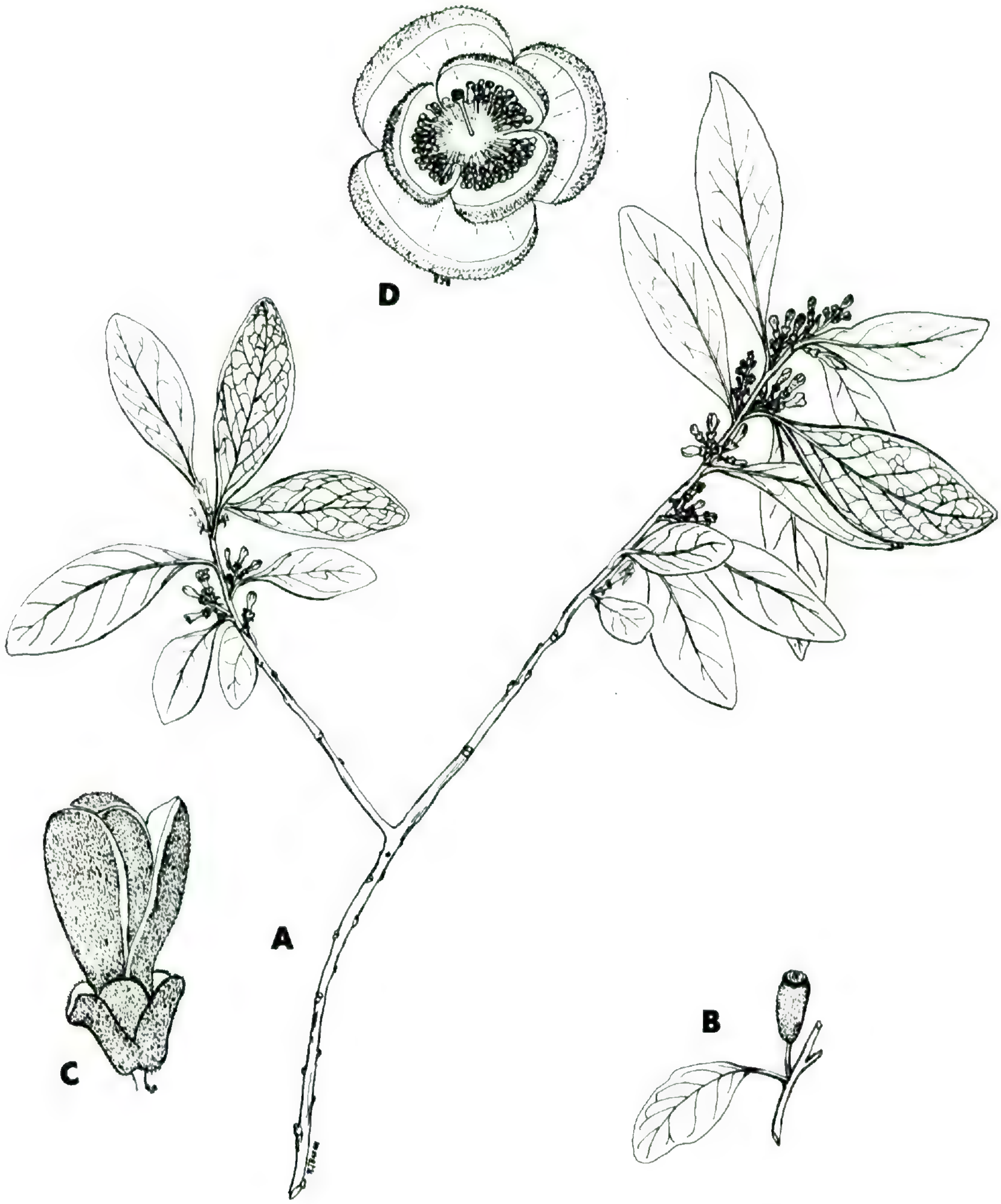

FIGURE 1. *Symplocos*.—A–B. *S. chiriquensis* Pittier.—A. Flowering branch (×½). [After *Allen 4717* (MO)]—B. Fruit, ?slightly immature. (×½). [After *Allen 4664* (MO).]—C–D. *S. serrulata* H. & B.—C. Flower (×3⅕).—D. Flower from above showing arrangement of stamens and petals (×6⅜₁₀). [After *Blum et al. 2416* (MO).]

Symplocos chiriquensis may be recognized by its small, glabrous, coriaceous leaves.

CHIRIQUÍ: Near Boquete, 4500–6500 ft, *Allen 4664* (MO). Ca. 1 mi SW of Boquete, 4000 ft, *Allen 4717* (MO, NY). Boquete, 3800 ft, *Davidson 739* (MO, US); 5500 ft, *Davidson 808* (MO, US). Savannas near Boquete, 4000 ft, *Davidson 843* (MO, US). Forests around Boquete, 1000–1300 m, *Pittier 2994* (NY, US). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1110* (MO). PANAMÁ: Cerro Campana, 2600 ft, *McDaniel 6829* (MO).

3. **Symplocos serrulata** H. & B., Pl. Aeq. 1: 190, *tab. 54.* 1808. TYPE: not seen. —FIG. 1C–D.

S. *tomentosa* H. & B., Pl. Aeq. 1: 195. 1808. TYPE: Herb. H.B.K. *38717* (P, not seen, MO, photo).
S. *irazuensis* Cufodontis, Arch. Bot. Sist. 9: 200. 1933. TYPE: Costa Rica, *Cufodontis 361* (F).

Trees to 10 m tall; twigs reddish tomentose, becoming blackish and scurfy with age, subtended by conspicuous leaf scars at the nodes. *Leaves* obovate, sometimes broadly so, apically short-acuminate with a well-defined drip tip, basally obtuse or rounded, the margins entire or minutely serrulate, slightly coriaceous, glabrous above and the midvein impressed, beneath softly ferrugineous with long wavy and curly yellowish and reddish brown hairs, the venation elevated, 6–8 prominent lateral veins on each side of the midvein; petiole 5–8 mm long, the glabrous upper side deeply impressed and the tomentose lower surface subterete. *Inflorescences* axillary, several-flowered congested fascicles; peduncles, pedicels, and bracts tomentose but mostly obscure. *Flowers* large for the genus, ca. 12 mm long; sepals ca. 5, rotund, 2 mm wide, 4 mm long, sericeous outside and ciliate; petals pinkish, reddish or bluish, ca. 6, 11 mm long, 5 mm wide, thick, dorsally canescent, apically cuculate, connate only at the very base but held together by the adnate staminal column, only the inner 4 with stamens; stamens ca. 95, adnate ca. 5 mm to the bottom of the corolla, the filaments separating into thick, straplike elements terminated by a short, ca. 1 mm long, slender stipe, the anthers rounded, ca. 0.5 mm across, the filaments glabrous, minutely muricate dorsally; ovary ca. 5-locular, emergent ca. ⅓ its length, densely tomentose on the flat top, the style basally hirsute with long, yellowish, acicular hairs, minutely tuberculate overall, the stigma an irregular capitate mass.

This species is widespread but perhaps rare in tropical America.

CHIRIQUÍ: Cerro Punta, 7000 ft, *Blum et al. 2416* (MO, PMA).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VIII

FAMILY 158. OLEACEAE[2]

W. G. D'ARCY[3]

Trees, *shrubs* or woody *vines*, evergreen or deciduous; pubescence of weak, simple hairs and usually of peltate glandular trichomes which in many groups are fused to the surfaces and present a punctate appearance. *Leaves* simple or pinnately compound, entire, lobed or serrate, pinnately veined, the undersides often punctate; mostly petiolate; exstipulate. *Inflorescences* in dichasial panicles or cymes, rarely solitary, mostly terminal; peduncles and pedicels bracteate. *Flowers* mostly perfect, often fragrant, pedicellate; calyx mostly cupular with 4–8 often somewhat unequal teeth; corolla mostly white or yellow but sometimes reddish, basally united into a tube, the limb obsolete, the 4–9 lobes usually forming more than half the corolla length, imbricate or valvate in bud; stamens 2(4), the filaments slender, inserted on the corolla tube, opposite one another and alternate with the corolla lobes, the anthers mostly oblong, the connective broad, apiculate, dehiscence longitudinal; style simple, apically divided into 2, mostly flat, deltoid to fusiform lobes, the lobes ventrally stigmatic, the ovary 2(–4)-carpellate and loculed with 1–2(–19) ovules in each locule, the ovules ascending or pendulous, anatropous or amphitropous. *Fruits* samaras, capsules or drupes, 1–4-seeded; seeds with a hard endocarp, albuminous or not. Chromosome numbers mostly $x = 23$ but differing in some genera.

This family includes some 400 species in 20–30 genera best developed in Asia. Of the 4 genera reported in Panama, only *Chionanthus* has species native to the New World and Panama.

The Oleaceae includes the important crop plant *Olea europaea* L. (olive, aceituno), and the important lumber trees *Fraxinus* (ash, fresnos). Many species are cultivated as ornamentals.

Literature:

Johnson, L. A. S. 1957. A review of the family Oleaceae. Contr. New South Wales Natl. Herb. 2: 395–418.

Knoblauch, E. 1892. Oleaceae. *In* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien. IV. 2: Wilhelm Engelmann, Leipzig.

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[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] I thank Peter S. Green and W. T. Stearn for reading this manuscript.

[3] Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis, Missouri 63110.

Taylor, H. 1945. Cyto-taxonomy and phylogeny of the Oleaceae. Brittonia 5: 337–367.

Wilson, K. A. & C. E. Wood. 1959. The genera of Oleaceae in the Southeastern United States. J. Arnold Arbor. 40: 369–384.

a. Corolla lobes many times longer than the tube and limb; united portion of corolla not exceeding the calyx; native trees ..... 1. *Chionanthus*
aa. Corolla lobes about as long as or shorter than the tube and limb; united portion of corolla much exceeding the calyx; cultivated or escaping trees, shrubs or vines.
b. Anthers exserted (Panama) ..... 3. *Ligustrum*
bb. Anthers included.
c. Corolla salverform, the tube narrow; cultivated and escaping vines and shrubs ..... 2. *Jasminum*
cc. Corolla urceolate, globose, the tube cupular; cultivated tree ..... 4. *Noronhia*

1. CHIONANTHUS

Chionanthus L., Sp. Pl. 1: 8. 1753; Gen. Pl., ed. 5. 9. 1754. TYPE: *C. virginicus* L.

Mayepea Aubl., Hist. Pl. Guiane 1: 81, *tab. 31.* 1775, nom. rejic. TYPE: *M. guianensis* Aubl. = *Chionanthus ligustrina* (Swartz) Pers.

Thouinia Thunb. ex L.f., Suppl. Pl. 89. 1781, nom. rejic., non Poit. 1804 (Sapindaceae). TYPE: *T. nutans* L.f.

Ceranthus Schreb., Gen. Pl. 1: 14. 1789, nom. rejic. TYPE: *C. schreberi* J. F. Gmelin.

Linociera Schreb., Gen. Pl. 2: 784. 1791, nom. cons., syn. prius *Mayepea* Aubl. et *Ceranthus* Schreb. TYPE: *Thouinia ligustrina* Swartz = *Chionanthus ligustrina* (Swartz) Pers.

Trees, deciduous or evergreen; twigs often with prominent lenticels. *Leaves* opposite, entire, pinnately veined, mostly glandular-punctate or with minute peltate trichomes beneath, sometimes with simple hairs as well; petioles slender; exstipulate. *Inflorescences* mostly terminal panicles, the branching opposite, dichasial; scalelike bracts and bracteoles present. *Flowers* mostly white, sometimes drying yellowish; calyx cupular or funnelform, mostly with 4 deltoid lobes; corolla with a short tube and ca. 4 elongate, linear, straplike petals; stamens 2, inserted opposite one another near the top of the corolla tube between the petals, the filaments short and glabrous, the anthers oblong to ellipsoidal, latrorse with a broad connective produced into an apicule or umbo; style short, cylindrical, apically 2-lobed, the lobes ventrally stigmatic, sometimes basally connate, the ovary 2-loculed with 2 pendulous ovules in each locule. *Fruits* ellipsoidal or oblong, 1-seeded drupes.

This genus may be recognized by its showy panicles of white flowers with linear petals. Until recently, tropical members of the genus, which are mostly evergreen, have been considered generically distinct from those of temperate North America and Asia which are deciduous. Decision to unite the 2 genera follows arguments proposed by Stearn (1976). The genus includes some 3–4 species from north temperate regions and over 100 from the tropics of both hemispheres. Bark of the roots has had some medicinal repute in the past.

Literature:

Stearn, W. T. 1976. Union of *Chionanthus* and *Linociera* (Oleaceae). Ann. Missouri Bot. Gard. 63: 355–357. [1977].

1. **Chionanthus panamensis** (Standley) Stearn, Ann. Missouri Bot. Gard. 63: 356, 1976 [1977].—FIG. 1.

Linociera panamensis Standley, Publ. Field. Columbian Mus., Bot. Ser. 8: 32. 1930. TYPE: Panama, Flat Rock, region of Almirante, Bocas del Toro, *Cooper 553* (F, not seen).

Trees to 15 m tall; twigs slightly compressed, drying black with prominent lenticels, minutely puberulent, especially at the nodes. *Leaves* elliptical, to 10 cm long, apically acuminate or obtuse, basally acuminate, the midvein prominent, the lateral veins, ca. 5 on each side, sometimes obscure above, reticulate beneath, appearing glabrate but with a few scattered hairs along the length and in domatia near the axils of the lower veins, and generally vestite with scattered, minute, subsessile, peltate, scutellate glandular trichomes. *Inflorescences* open, many-flowered, dichasial panicles to 10 cm long, pyramidal to globose, mostly with a definite axis, the branches and pedicels subtended by narrow, scalelike bractlets; pedicels 1–3 mm long, angled, minutely puberulent, sometimes with 1–2 minute scalelike bracteoles along the length. *Flowers* showy, odorous (Standley); calyx glabrate, funnelform, ca. 1 mm long, 4-lobed to ca. halfway down, the lobes deltoid; corolla white, the tube not exceeding the calyx, the lobes mostly 4, linear, straplike, 1–2 mm wide, 10–20 mm long, often unequal; stamens 2, the filaments short, inserted between the corolla lobes near the top of the tube, opposite one another, the anthers oblong, the thecae latrorse, the connective broad with a bent and ventrally transposed apical umbo; style short, cylindrical, apically 2-lobed, the lobes ventrally stigmatic, the ovary glabrous. *Fruits* (Standley) white, compressed, elliptical drupes ca. 2 cm long, 1 cm wide, acute on each end, veined on each side.

This species is known only to lowland Panama and Costa Rica. Standley noted that the flowers and burning wood have the odor of roses.

COCLÉ: Cerro Pajita, 3000 ft, *Allen 4498* (MO, US). PANAMÁ: Loma Larga beyond Cerro Azul, *Dressler 3420* (MO).

2. JASMINUM

Jasminum L., Sp. Pl. 7. 1753; Gen. Pl., ed. 5. 7. 1754. TYPE: *J. officinale* L.

Shrubs or woody *vines*, sometimes deciduous; stems, mostly terete; pubescence of simple hairs. *Leaves* alternate or opposite, simple, trifoliolate or pinnately compound; blades entire or lobed; petioles short, sometimes articulated; stipules wanting. *Inflorescences* mostly terminal, sometimes on short spurs, cymose, dichasial panicles or heads; bracts and bractlets mostly present; pedicels mostly short or wanting. *Flowers* often fragrant, heterostylous; calyx campanulate, cupular or funnelform, with 5–8 slightly unequal teeth; corolla white or yellow, rarely reddish, mostly drying yellowish or brownish, salverform, the tube slender, elongate, often curved, the limb obsolete, the lobes imbricate, 4–many, sometimes in several whorls, mostly narrowly elliptical; stamens 2, included, the short, glabrous filaments inserted near the middle of the corolla tube and opposite one another, the anthers oblong, introrse, basifixed, the connective broad, extended

FIGURE 1. *Chionanthus panamensis* (Standley) Stearn. Habit (×⅗). [After *Dressler 3420* (MO).]

into a short apicule; stigmatic style branches fusiform, included or long-exserted, the ovary hemispherical or truncate, the 2 carpels mostly demarcated by a sulcus or separating plate of nonaccrescent tissue, the ovules 1–4 in each locule, mostly ascending, amphitropous, sometimes pendulous and anatropous. *Fruits* of 2 drupe-

lets, connate or divaricate, juicy or fleshy, 1–2-seeded, one drupelet often abortive; pyrenes with little endosperm.

Jasminum is a genus of over 200 species native to the Old World, mainly of tropical regions. Over 30 species are cultivated in the Americas and many of these have become naturalized. In Panama five species are now known to have been cultivated, but others may be introduced and cultivated from time to time. Plants in this genus are commonly cultivated for their attractive form and foliage, their showy flowers, and the pleasant scent of the flowers. In other countries species of jasmine are used for perfumery and for scenting tea. Common names are "jasmine" (English), "jasmin" (Spanish).

Literature:

Dandy, J. E. 1950. Oleaceae. Kew Bull. 5: 368. [1951].
Green, P. S. 1965. Studies in the genus *Jasminum* III. The species in cultivation in North America. Baileya 13: 137–172.
Kobuski, C. E. 1959. A revised key to the Chinese species of *Jasminum*. J. Arnold Arbor. 40: 385–390.
Merrill, E. D. 1923. *Jasminum*. Enum. Philippine Pl. 3: 306–309.

a. Leaves compound or deeply lobed.
  b. Inflorescences pubescent; calyx lobes short-deltoid; leaves trifoliolate .. 2. *J. fluminense*
  bb. Inflorescences glabrate; calyx lobes slender, elongate; leaves lobed or mostly 5–7-foliolate ..... 3. *J. grandiflorum*

aa. Leaves simple, entire.
  c. Calyx lobes copiously pubescent, filiform ..... 4. *J. multiflorum*
  cc. Calyx glabrate, slender, but not filiform.
    d. Petioles articulated just below the middle; corolla lobes mostly in 1 whorl of 5–8 lobes; leaves glabrous ..... 1. *J. dichotomum*
    dd. Petioles not articulated; corolla lobes numerous in 2 or more whorls; leaves pubescent ..... 5. *J. sambac*

1. **Jasminum dichotomum** Vahl, Enum. Pl. 1: 26. 1804. TYPE: not seen.

Scrambling *shrubs* to 2.5 m tall; twigs sinuous, flattened and furrowed, minutely puberulent on emerging, soon glabrous, solid. *Leaves* opposite, simple (ternate), entire, ovate or elliptical, sometimes rotund, apically short, acuminate or acute, basally rounded or obtuse, coriaceous, the midvein impressed above, elevated beneath, the lateral veins 6–7 on each side, obtuse to the midvein, glabrous on both sides, minutely (under ×45 magnification) punctate beneath; petioles 10–30 mm long, canaliculate and pubescent above, glabrous beneath, articulated below the middle. *Inflorescences* terminal, small, more or less congested, dichasial panicles, the dichotomies marked by conspicuous ridges; peduncles 15–30 mm long; pedicels 2–5 mm long, minutely pubescent, subtended by scalelike bractlets. *Flowers* fragrant; calyx glabrate, the cup 3 mm tall, the teeth 5–7, often unequal, 5–6 mm long, linear but appearing succulent; corolla white drying orange brown, salverform, the tube ca. 2 cm long, the lobes thick, ca. 10 mm long. *Fruits* ellipsoidal, maturing black, 12–14 mm long, assymetrical.

This species is native to tropical Africa. It has recently been introduced to the New World and has become naturalized in Florida.

CANAL ZONE: Cultivated, Summit Gardens, *Croat 9058*, (K, MO, PMA).

2. **Jasminum fluminense**[4] Vell., Fl. Flum. 10. 1825; Atlas 1: *tab* 23. 1827 (1835). TYPE: Brasil, Isla Sta. Cruz, Rio de Janeiro, *Vellozo*, not seen.

J. azoricum mult. auct., non L.

Scandent *shrubs* to 3 m tall; branches solid, slender, terete, puberulent to tomentose with curled, simple hairs. *Leaves* opposite, trifoliolate, to 9 cm long; leaflets ovate, apically acuminate, acute or obtuse, basally subcordate, truncate, or short acuminate, the veins ca. 5 on each side, arcuate, not anastomosing at the margins, above pubescent on and near the midvein, otherwise glabrate, beneath glabrate except for tufts of tomentum in the axils of the lower veins; petiolules and petioles tomentose, the terminal petiolule and petiole about equal, 15–20 mm long, angled, the later petiolules shorter, 4–10 mm long. *Inflorescences* more or less open terminal panicles 4–15 cm long with several flowers opening at a time; petioles mostly 2–3 cm long, puberulent to tomentose, subtended by pairs of short, linear bracts ca. 3 mm long; pedicels 2–4 mm long, subtended by short, linear, tomentose bracts and often with 1 or 2 minute bractlets on the lower half. *Flowers* fragrant, heterostylous; calyx 2–3 mm long, cupular, as broad as long, glabrate to tomentose, the short teeth 1 mm long; corolla white, drying yellowish, salverform, the tube 15–30 mm long, slightly expanded apically, the lobes narrow, 10–15 mm long; style branches fusiform, ca. 5 mm long, slightly exserted, the ovary subtruncate, slightly sulcate. *Fruits* pairs of ellipsoid, divaricate, baccate drupelets ca. 7 mm across; pyrenes not seen.

Although a native of Africa, this species was first described from Brasil where it had become naturalized following early Portuguese introduction. It has long been known under the name *J. azoricum* L., a species which differs in having glabrate inflorescences, longer pedicels, and usually longer corolla tubes. *Jasminum fluminense* is widely cultivated in tropical gardens. Common names are "jasmin de novia," "jasmin cafe" (Hispaniola).

PANAMÁ: Isla Chepillo, *Duke 10314* (OS). Sabanas, *Paul 282* (US).

3. **Jasminum grandiflorum** L., Sp. Pl., ed. 2. 9. 1762. TYPE: Eastern Asia, Herb. Linn (LINN 17.2, not seen, MO, microfiche).—FIG. 2.

J. officinale L. var. *grandiflorum* (L.) Stokes, Bot. Comment. 1: 21. 1830.
J. officinale f. *grandiflorum* (L.) Kobuski, J. Arnold Arbor. 13: 161. 1932.

Sprawling *shrubs* to several m long; branches slender, weak, terete, ridged or grooved, mostly solid. *Leaves* pinnate, lobed or dissected, mostly 5–7-foliolate, to 8 cm long, 3–6 cm wide; leaflets ovate, apically acute, obtuse or rounded, sometimes mucronulate, basally obtuse, rounded or truncate, glabrate, the mid-

[4] For a list of synonyms see Dandy (1950). Only the names noted here have been used for Panamanian material.

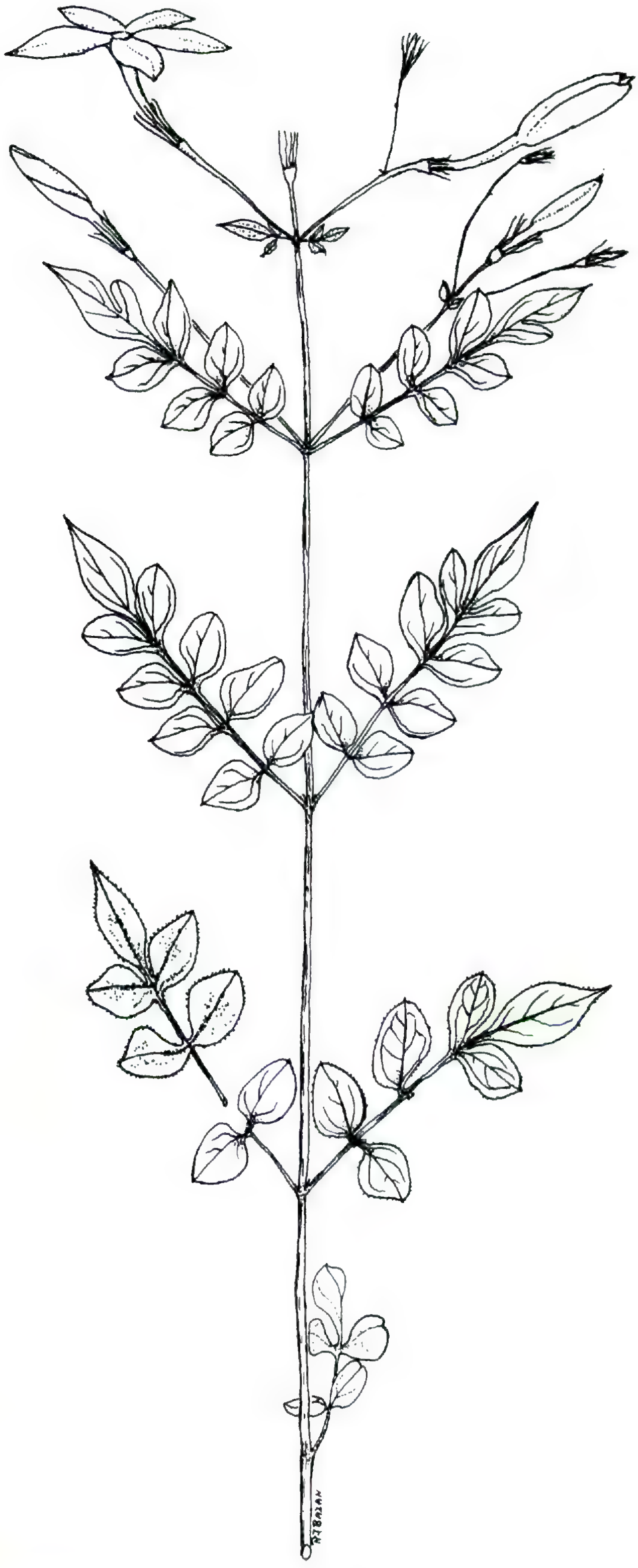

FIGURE 2. *Jasminum grandiflorum* L. Habit (×⅘). [After *Maurice 757* (US).]

vein prominent, the minor venation obscure; petiole 1–4 cm long, glabrous, the rachis sometimes narrowly winged; petiolules short or wanting, basally pubescent in the axil. *Inflorescences* few-flowered, terminal cymes, the terminal peduncle shorter than those subtending it, sometimes with entire, foliaceous bracts; peduncles 1–2 cm long, slender, demarcated from the similar, 5–15 mm long pedicels by minute bractlets. *Flowers* fragrant; calyx cup 1–3 mm long, glabrous, the lobes linear, glabrate, to 10 mm long; corolla white, drying yellowish, salverform, the tube 15–20 mm long, slender, sometimes curved, the lobes mostly 5, narrow, 15–25 mm long. *Fruits* not seen.

This species is native to subtropical regions of Southwest Asia. It is quite similar to *J. officinale* L., differing in having larger flowers, slightly different inflorescence structure, and in not being cold-hardy. In southern France *J. grandiflorum* is cultivated for the perfume industry.

PANAMÁ: Villa Cáceres, Cuidad de Panamá, *Carrasquilla 243* (MO). In garden, Panama City, *Maurice 757* (US). Town of Taboga, Taboga Island, *Mori et al. 4082* (MO).

4. **Jasminum multiflorum** (Burm. f.) Andrews, Bot. Rep. 8: *tab. 496.* 1807.

Nyctanthes multiflora Burm. f., Fl. Ind. 5, *tab. 3, fig. 1.* 1768.
N. pubescens Retz., Obs. Bot. 5: 9. 1788. TYPE: Calcutta, *Konig* (?LD, not seen).
Jasminum pubescens (Retz.) Willd., Sp. Pl. 1: 37. 1797 (1798).

Scrambling *shrubs* to 6 m tall; branching mostly opposite, the branches subtended by ridges resembling stipular scars, the twigs tomentose, sometimes in lines; pubescence of yellowish, crinkly, simple hairs. *Leaves* simple, entire, to 5 cm long, ovate to cordate, apically acuminate, acute, obtuse or rounded, often mucronulate, basally cordate or truncate, the lateral veins 4–5 on each side, ascending-arcuate, not anastomosing at the margins, the major veins prominent and tomentose beneath, above glabrate but pubescent on the major veins and near the margins, beneath evenly pubescent overall with curved yellowish hairs; petioles short, ca. 5 mm long, tomentose, articulated near the middle. *Inflorescences* terminal or axillary, a congested panicle or capitulum, many-flowered; peduncles tomentose; pedicels short or wanting. *Flowers* fragrant, heterostylous; calyx of 5–8 linear, 8–12 mm long, long-pubescent teeth; corolla white, drying brownish, salverform, the tube 15–20 mm long, sometimes curved, the lobes narrowly elliptical, 15–20 mm long, to 10 mm wide; anthers ca. 5 mm long; style branches exserted, fusiform, the 2 carpels separated by a prominent sterile plate. *Fruits* not seen.

This species is commonly cultivated in tropical gardens for its attractive flowers and powerful, pleasant scent. It is a native of Southeast Asia. A common name is "jasmin del papel."

CANAL ZONE: Hospital grounds at Ancón, *Pittier 2738* (US). Balboa, *Standley 26989* (US). Cultivated, Mount Hope Cemetery, *Standley 28775* (US).

5. **Jasminum sambac** (L.) Ait., Hort. Kew., ed. 1, 1: 8. 1789.

Nyctanthes sambac L., Sp. Pl. 6. 1753. TYPE: Herb. Linn. (LINN 16.2, not seen, MO, microfiche).

Shrubs, or woody *vines* to 2 m high, much branched; twigs terete or slightly compressed, sometimes hollow, often with a prominent groove, puberulent with weak, ascending hairs. *Leaves* opposite, verticillate, or subopposite, to 6 cm long, 5 cm wide, simple, entire, rotund, elliptical or obovate, rounded or obtuse at each end, chartaceous, the midvein impressed above, elevated beneath, the 4–6 pinnate veins on each side prominent, arcuate, attenuate, glabrate above except on the major veins, puberulent beneath with minute, erect hairs; petiole 2–5 mm long, pubescent, curved and thicker upwards. *Inflorescences* small, with mostly only a few flowers opening at a time; peduncles compressed, tomentose or glabrate, the pedicels 3–20 mm long, with small, narrow bracts and bractlets. *Flowers* fragrant; calyx of 5–12 porrect, linear lobes with a narrow membranous apiculus, to 7 mm long, green; corolla white, salviform-cyathiform, the tube 7–12 mm long, stout, the lobes somewhat exceeding the tube, mostly in double or triple whorls (single in some wild Indian populations); stamens 2, but androecium and gynoecium often reduced to minute, petaloid processes. *Fruits* not seen.

This species is native to India. It is a widespread tropical ornamental. Common names are "Arabian jasmine," "jasmin de Arabia," "diamela."

CANAL ZONE: Without other locality, *Johansen* 2 (US).

3. LIGUSTRUM

Ligustrum L., Sp. Pl. 7. 1753; Gen. Pl., ed. 5. 8. 1754. TYPE: *L. vulgare* L.

Shrubs or small *trees*, evergreen or deciduous; pubescence of simple hairs. *Leaves* simple, entire, opposite, pinnately veined, often minutely punctate beneath; petioles short, canaliculate; exstipulate. *Inflorescences* mostly terminal panicles, sometimes congested and spikelike, the branching sometimes alternate; scalelike bracts and bractlets mostly present. *Flowers* often odorous, mostly white; calyx small, cupular, 4-denticulate; corolla salverform to campanulate, lobed ca. halfway, the 4 lobes valvate but sometimes appearing imbricate when dry; stamens 2, the slender filaments inserted near the top of the corolla tube, the anthers basifixed, oblong, apiculate, introrse; style with 2 oblong or fusiform stigmatic branches, the ovary subglobose, 2-carpellate and 2-loculed, each with 2 pendulous, anatropous ovules. *Fruits* baccate drupes with 1–4 pyrenes, rarely dehiscent.

This genus is native to the Old World and is best developed in eastern Asia. Several species are cultivated in the New World and some of these are naturalized. Privets are useful hedge plants. In some places they are difficult to control because of their vigorous underground growth. A few cases of livestock poisoning have been attributed to this genus in other parts of the world. Common names are "privet" (English) and "alagustre" (Spanish).

1. **Ligustrum sinense** Loureiro, Fl. Cochinch. 19. 1790. TYPE: China, Canton, *Louriero* (?BM, not seen).

   Much branched *shrubs* to 5 m tall; twigs terete, tomentose with short, weak, simple hairs, the older twigs with prominent, white lenticels. *Leaves* opposite,

simple, entire, elliptical or ovate, to 6 cm long, apically obtuse, acute, or rounded, mucronulate, basally obtuse, the midvein impressed above, elevated and prominent beneath, the lateral veins 5–7 on each side, often obscure above, glabrous on both sides except on the major veins and a few hairs on the lower margins, often drying darker above, minutely glandular-punctate beneath; petiole 2–4 mm long, canaliculate, pubescent. *Inflorescences* terminal, spikelike, many-flowered panicles, to 7 cm long, the branching alternate; peduncles short, angled, pilose, bracteate; pedicels 1–2 mm long, flattened with sharp angles, glabrous, subtended by minute, cuculate, glabrous scalelike bractlets. *Flowers* odorous; calyx cupular, glabrous, ca. 1.5 mm tall, the apex sinuate-dentate; corolla white, sometimes drying purplish, ca. 5 mm long, campanulate, lobed about halfway, the tube expanding upwards, the lobes 4, valvate, obtuse; stamens 2, the filaments inserted at the top of the tube, opposite one another and alternate with the corolla lobes, the filaments exserted, glabrous, the anthers oblong, apiculate; style branches fusiform, slightly exserted, the style and ovary glabrous. *Fruits* black, baccate drupes ca. 5 mm across, elliptical.

A native of China, this species is widely cultivated in warm temperate regions as a landscaping hedge. The showy white flowers have a strong odor offensive to some people.

CHIRIQUÍ: Guadalupe, 1.5 km N of Cerro Punta, *Mori & Kallunki 5719* (K, MO, PMA).

4. NORONHIA

Noronhia Stadman in Thouars, Gen. Nov. Madag. 8. 1806. Based on *Olea emarginata* Lam. = *Noronhia emarginata* (Lam.) Stadman.

Trees[5], branches often stout, smooth, mostly glabrous. *Leaves* persistent or deciduous, opposite, rarely verticillate, entire or emarginate, often coriaceous, sometimes punctate, the venation pinnate, often obscure, the minor venation obscure; bud scales sometimes hairy; petioles mostly short, stout, sometimes contrasting in color with the leaf and stem. *Inflorescences* axillary or falsely terminal, mostly short panicles or racemes, sometimes fascicles or solitary, subtended by small bracts at the dichotomies; pedicels often stout, subtended by bractlets. *Flowers* perfect, 4-merous; calyx small, campanulate, the lobes deltoid or obtuse, often unequal and the outer pair overlapping in bud; corolla thick, glabrous, valvate, drying dark, urceolate, cyathiform, campanulate or rotate, the tube sometimes much reduced and the limb and lobes spheroidal, the base inside forming a flat platform or with an elevated coronule (nectary) surrounding the fertile parts; stamens 2(4), inserted on the tube, the anthers large, compressed, basifixed, subsessile, dehiscing laterally, rarely introrsely; ovary conical, glabrous, bilocular with 2 anatropous, pendulous, axile ovules in each locule, one ovule aborting, the style short or wanting, the stigma short, thick, 2-lobed. *Fruits* globose or pointed, stoney drupes; seeds large, the raphe ramified and conspicuous against the integument, the endosperm wanting, the cotyledons plano-convex, thick, the radicle superior, conical, short and thick.

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[5] Description adapted in part from Perrier (1952).

The anthers, stigma, and coronule, when present, all rise to about the same level just above the floor of the corolla. The fruit includes a large seed flanked by a large membranous body, the abortive locule; sometimes the abortive ovules can be seen.

Long believed to be monotypic or nearly so, the genus was revised by Perrier (1952) who recognized 41 species and several varieties. *Noronhia* is endemic to Madagascar and the Comores Islands. It is closely related to *Schrebera* Roxb. of Africa and the Indian Ocean region.

Literature:

Perrier de la Bathie, H. 1952. Oléacées. *In* H. Humbert, Flore de Madagascar et les Comores. Gouvernement général de Madagascar, Paris.

1. **Noronhia emarginata** (Lam.) Stadman in Thouars, Gen. Nov. Madag. 8. 1804.

Olea emarginata Lam., Tabl. Encycl. Méth. 1: 29, *tab. 8, fig. 2a, 2b.* 1791. TYPE: Madagascar, *Martin* (not seen).

Trees to 15 m tall, bark smooth; branches stout, terete, the terminal twigs flattened. *Leaves* elliptical or obovate, to 16 cm long, 10 cm wide, entire or emarginate, mucronulate, basally narrowed or obtuse, above blue green with contrasting pinnate veins which anastomose to form a continuous vein ca. 5 mm from the revolute margin, beneath yellow green, minutely punctate, the lateral venation obscure; petiole stout, ca. 5 mm thick, 10–15 mm long, light brown and contrasting with the color of the leaves and stems. *Inflorescences* small racemes or panicles to 8 cm long, lateral on horizontal or descending twigs; pedicels and peduncle stout, green, subtended by minute deltoid or obtuse, deciduous bracts; pedicels 7–15 mm long, the base of the flower with 2 opposite, minute, appressed bracteoles. *Flowers* self-fertile, 4-merous; calyx lobes similar, obtuse, ciliolate, ca. 1.5 mm long; corolla yellow, drying dark, thick and fleshy, the tube obscure, the limb lobed over halfway, the limb and lobes cuculate, globose, 6–7 mm across, the interior base flat and the coronule scarcely evident; stamens subsessile, inserted on the corolla tube, the anthers green, becoming dark brown after anthesis, dorsiventrally compressed, appressed to the ovary, broadly elliptical with a strong lateral sulcus, ca. 2 mm long, opening laterally; ovary green, conical, 2–3 mm long, smooth, glabrous, 2-locular with 2 ovules in each locule, the stigma white, glistening, 2-lobed, sessile on the ovary apex, the stigma and anther tips at the same level just above the floor of the corolla. *Fruits* globose to turbinate, apiculate, ca. 20 mm long, drying hard, dark brown, slightly rough; seed pyriform, dark russet, 10–12 mm long, only partly filling the abortive locule, the cotyledons unequal.

This species is occasionally cultivated throughout the lowland tropics as a street or specimen tree. The fruit is said to be edible, and the wood hard. The gray green, coriaceous, *Clusia*-like leaves give it a distinctive appearance. The

small, yellow flowers are usually borne near the ends of curved, horizontal or descending twigs. *Noronhia emarginata* is native to Madagascar.

CANAL ZONE: Summit Garden, *Croat 13822* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 176. LENTIBULARIACEAE

PETER TAYLOR[2]

Herbs, annual or perennial, aquatic, terrestrial or epiphytic with special vegetative organs adapted for the capture and digestion of small organisms; roots sometimes absent. *Leaves* rosulate or absent, often replaced by somewhat leaflike, entire or dissected photosynthetic organs which are in fact modified stems. *Inflorescences* terminal or lateral, pedunculate, racemose or scapose, simple or rarely branched, bracteate or ebracteate, often with barren bracts (scales) on the peduncle; bracteoles 2 or 0, usually at the base of the pedicels. *Flowers* hermaphrodite, zygomorphic; calyx deeply 2-, 4- or 5-partite, almost regular or 2-lobed, the sepals sometimes free to the base, persistent and often accrescent; corolla gamopetalous, 2-lipped, usually spurred, rarely saccate, mostly shades of violet or yellow, the upper lip entire or ± 2-lobed, the lower lip entire or 2–5-lobed, usually with a raised ± gibbous palate; stamens 2, inserted at the base of the corolla; ovary superior, 1-locular, the style usually short, the stigma 2-lipped, the placenta free central or free basal, the ovules 2 or usually numerous. *Fruits* valvate, circumscissile or indehiscent capsules; seeds 1 or usually numerous, mostly small, variously shaped.

This family includes 4 genera with about 250 species of temperate and tropical regions. Two genera occur in Panama. Keys and descriptions are not necessarily based on Panamanian material which is sparse—most of the species are relatively, or very, widespread in America.

a. Calyx 5-lobed; terrestrial scapose herbs with rosulate leaves, the upper surface of which is provided with viscid glands which trap and digest small insects ..... 1. *Pinguicula*
aa. Calyx 2-lobed; aquatic, terrestrial or epiphytic herbs with simple or dissected ± leaflike photosynthetic organs, pedunculate racemose inflorescences, and submerged or subterranean stolons bearing small bladderlike traps ..... 2. *Utricularia*

1. PINGUICULA

Pinguicula L., Sp. Pl. 17. 1753; Gen. Pl., ed 5. 11. 1754. TYPE: *P. vulgaris* L.

Annual or perennial *herbs* of damp places, scapose with numerous filiform roots. *Leaves* radical, entire, sessile or petiolate, ± fleshy, covered on the upper surface with sessile and stipitate viscid glands which capture and digest small

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[1] Assisted by National Science Foundation Grant BMS 72-0441 A03 (Thomas B. Croat, principal investigator).

[2] Royal Botanic Gardens, Kew, England.

organisms. *Pedicels* erect, ebracteate. *Flowers* solitary; calyx 5-fid, ± bilabiate; corolla yellow, white or various shades of pink to purple or blue, limb ± bilabiate, the upper lip 2-lobed, the lower lip 3-lobed, the lobes entire to ± deeply bifid, or rarely the limb ± regularly 5-lobed, the spur short to very long; stamens short, the filaments incurved, the anthers globose; ovary ± globose, glandular, the ovules numerous. *Capsules* ± globose, laterally bivalvate or dehiscing irregularly; seeds minute, oblong, rugose.

This is a widespread genus of about 45 species distributed throughout the north temperate and mediterranean regions, the Himalayas, southeastern United States, and Central and South America. One species occurs in Panama.

1. **Pinguicula crenatiloba** DC., Prodr. 8: 30. 1844. TYPE: Mexico, *Sessé & Moçino s.n.* (F, MO, photos).—FIG. 1.

Perennial very small *herbs*, 1.5–6 cm high. *Leaves* 5–8, obovate, the apex rounded, the margin narrowly involute, 5–12 mm long, pale green. *Pedicels* erect, filiform, stipitate-glandular. *Flowers* 4–6 mm long; calyx ± bilabiate, externally stipitate-glandular, the upper lip trilobed to about half its length, the lower lip bilobed; corolla pale mauve or white, bilabiate, the upper lip 1–2.5 mm long, bilobed, the lower lip rhomboid, 3–4 mm long, trilobed, the lobes emarginate, the midlobe longer than the lateral lobes, the palate lunulate or obscurely bigibbous, covered with clavate hairs, the spur cylindrical, the apex obtuse, 1.5–2.5 mm long. *Capsules* globose, 1.5–2 mm in diam.; seeds ellipsoid, ca. 0.3 mm long.

This species occurs in Mexico, Guatemala, Honduras, El Salvador, and Panama.

This tiny plant is probably often overlooked and quite possibly much commoner and more widespread in Panama than the few available specimens would indicate.

CHIRIQUÍ: Boquete, 3300–4200 ft, *Lewis et al. 327* (MO). Trail from San Félix to Cerro Flor, 100–850 m, *Allen 754* (MO, NY). PANAMÁ: Cerro Campana, *Dressler 4515* (J). VERAGUAS: Río San Juan, *Correa et al. 1941* (K).

2. UTRICULARIA

Utricularia L., Sp. Pl. 18. 1753; Gen. Pl., ed. 5. 11. 1754. TYPE: *U. vulgaris* L.

Herbs, annual or perennial, aquatic, terrestrial or epiphytic, always of damp places, without true roots or leaves but with stems modified in various ways to function as tubers, rhizoids, stolons, and ± leaflike photosynthetic organs, all species bearing small complex bladderlike traps for the capture and digestion of small organisms. *Inflorescences* pedunculate, racemose, usually simple, bracteate, sterile bracts (scales) often present on the peduncle and sometimes also on the inflorescence axis; bracts varied, basifixed, medifixed or variously produced below the point of insertion; bracteoles 2 or absent, rarely connate with the bract. *Flowers* with the calyx 2-lobed, usually accrescent; corolla usually spurred, yellow or various shades of violet or purple, or white, rarely red, the upper lip entire or ± 2-lobed, the lower lip entire or 2–5-lobed; stamens usually short, the

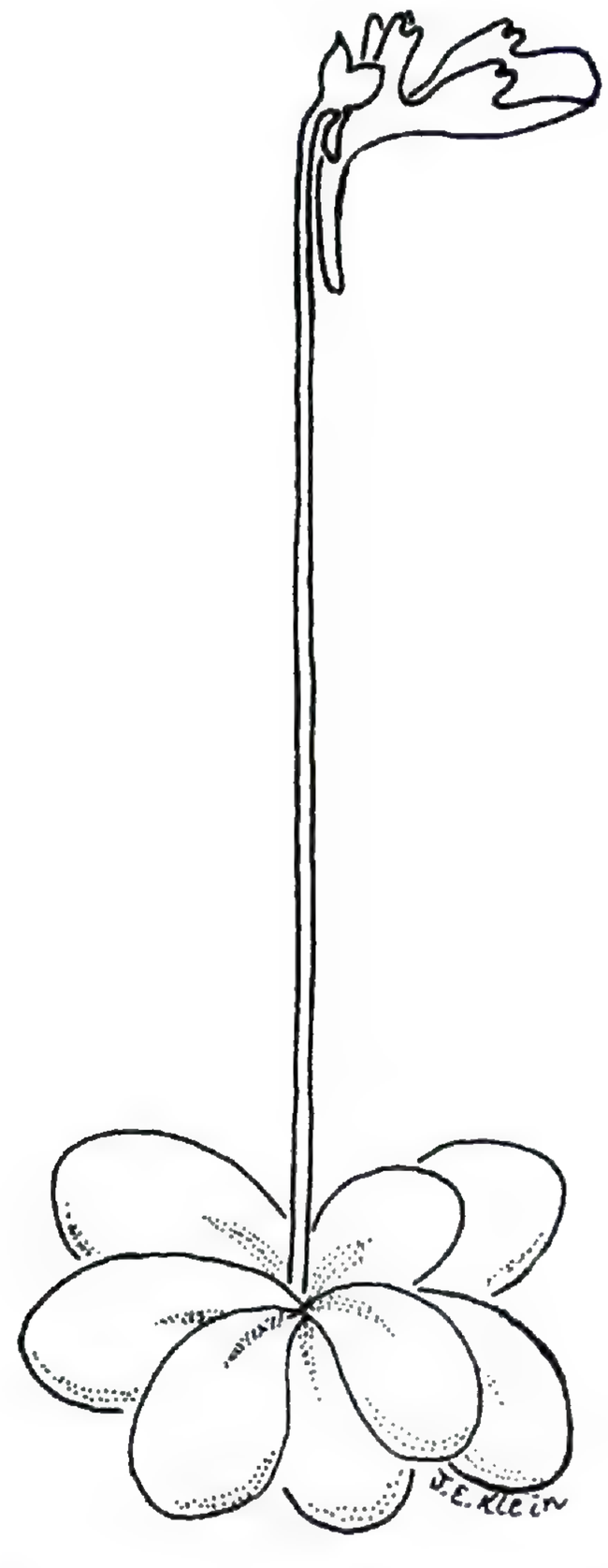


FIGURE 1. *Pinguicula crenatiloba* DC. Habit (×3). [After *Allen 754* (MO).]

filaments often winged, the anthers globose or ovoid; ovary ± globose, the ovules 2–many. *Capsules* globose to ovoid, dehiscing variously by longitudinal slits, dorsiventral or lateral valves or pores, circumscissile or indehiscent; seeds 1–many, variously shaped.

This is a widespread but mainly tropical genus of ca. 180 species, most diverse and abundant in seasonally wet savanna type vegetation. A few species are epiphytic. This group is most highly developed in the mountains of South and Central America and accounts for 5 of the 12 species recorded in Panama. The remaining 7 Panamanian species are all more or less widespread in the New World and 3 of these occur also in tropical Africa. A further, unascertained Panamanian species, not included in the key, is represented by incomplete, indeterminable material. It is included at the end of this generic treatment as *U.* sp.

The morphology of the vegetative parts of *Utricularia* is peculiar and has been the subject of numerous detailed studies. An admirable summary and bibliography is published by Lloyd (1942). The true nature of the leaflike organs is discussed by McIntyre & Chrysler (1943).

The stolons usually radiate from the base of the inflorescence and are usually relatively robust in the aquatic species but delicate and hidden in the substrate

in the terrestrial and epiphytic species. They are often branched and from them arise the photosynthetic organs and traps. The rhizoids are specialized, rootlike organs which are present in some species, both aquatic and terrestrial, and they always arise from the base of the inflorescence. The photosynthetic organs are numerous and obvious in most aquatic species and divided in capillary segments, while those of the terrestrials and epiphytes are mostly entire, sometimes very small or completely absent or sometimes well developed and leaflike. The traps are extremely complex and their morphology provides useful taxonomic characters. They range in size from 0.2–6 mm, are mostly globose or ovoid, and are more or less stalked with the mouth adjacent to the stalk (basal), opposite the stalk (apical), or at some intermediate position (lateral). The mouth is often provided with processes on the upper and/or lower lips. The two calyx lobes are sometimes similar or often markedly dissimilar. The corolla is bilabiate with a usually closed throat and no tube. The upper lip is mostly ovate, entire or 2-lobed, and the lower lip is usually larger, often with a prominent gibbous palate and an entire or more usually 2–5-lobed limb. A spur is usually well developed but sometimes short and saccate. The two stamens are inserted at the base of the upper lip, and the anther thecae are distinct or confluent. The stigma is 2-lobed with the lower lobe usually much larger.

Literature:

Casper, S. J. 1966. Monographie der Gattung *Pinguicula* L. Biblioth. Bot. 127/128: 1–209, *Tafn. 1–16.*

Fernández-Pérez, A. 1964. Lentibulariaceae de Colombia y Perú. Caldasia 9: 5–79.

Gibson, D. Nash. 1974. Lentibulariaceae. *In* Flora of Guatemala. Fieldiana, Bot. 24 (3–4): 315–328.

Lloyd, F. E. 1942. The Carnivorous Plants. Chronica Botanica, Waltham, Massachusetts.

McIntyre, W. G. & M. A. Chrysler. 1943. The morphological nature of the photosynthetic organs of *Orchyllium endresii* (*Utricularia endresii*) as indicated by their vascular structure. Bull. Torrey Bot. Club 70: 252–260.

Taylor, P. 1964. The genus *Utricularia* L. (Lentibulariaceae) in Africa (south of the Sahara) and Madagascar. Kew Bull. 18: 1–245.

———. 1967. Lentibulariaceae. *In* Botany of the Guayana Highland. Mem. New York Bot. Gard. 17: 201–228.

———. 1975. Lentibulariaceae. *In* G. Harling & N. B. Sparre (editors), Flora of Ecuador. Opera Bot., Ser. B, 4: 9–21.

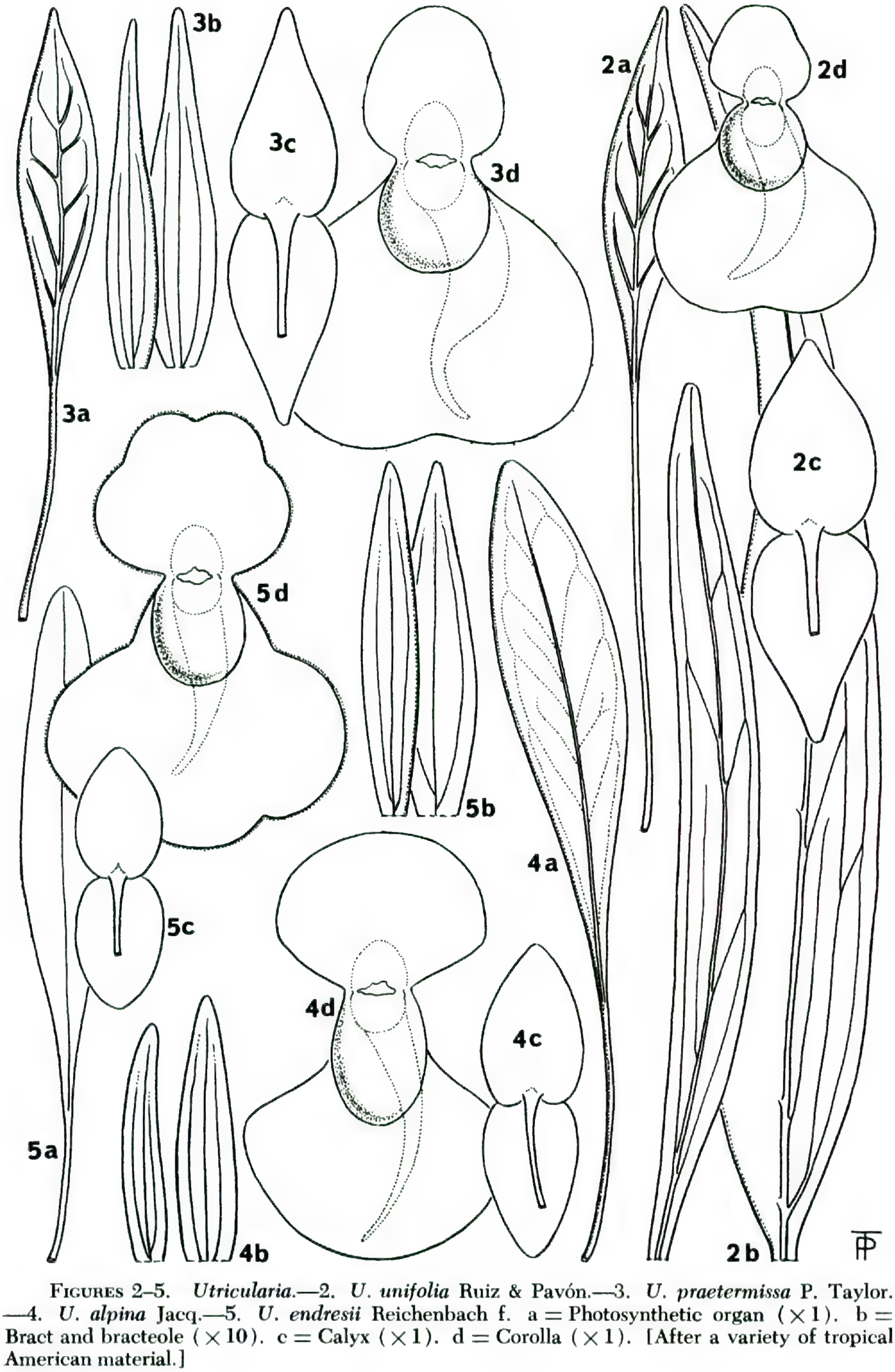
a. Terrestrial or epiphytic herbs; photosynthetic organs entire, sometimes well developed and leaflike, but often evanescent and decayed or inconspicuous at anthesis; bracteoles present (but sometimes connate with bract) or if absent then bracts medifixed.
  b. Bracteoles present, bract basifixed; corolla white, mauve or yellow.
    c. Epiphytic herbs, usually with well-developed leaflike photosynthetic organs present at anthesis; ovoid or fusiform tubers usually present at the base of the inflorescence; corolla shades of violet or white.
      d. Corolla 10–20 mm long, the lower lip deeply 3-lobed ..... 6. *U. jamesoniana*

dd. Corolla 30–50 mm long, the lower lip entire, emarginate or shallowly 3-crenate.
e. Margins of corolla densely stipitate-glandular, the lower lip 3-crenate; lamina of photosynthetic organs membranous, longer than the pseudopetiole ---------- 3. *U. endresii*
ee. Margins of corolla not or only sparsely stipitate-glandular, the lower lip entire or emarginate; lamina of photosynthetic organs coriaceous, shorter or longer than the pseudopetiole.
f. Bracts 10–30 mm long, usually falcate; upper lip of corolla not or scarcely wider than the upper calyx lobe, apex of the spur not deflexed; lamina of photosynthetic organs with conspicuous nerves, usually shorter than the pseudopetiole ---------- 12. *U. unifolia*
ff. Bracts usually less than 6 mm long, straight; upper lip of corolla as wide as or wider than the upper calyx lobe, apex of the spur deflexed or not; lamina of photosynthetic organs with or without conspicuous nerves, often longer than the pseudopetiole.
g. Apex of corolla spur deflexed, the upper lip about as wide as the upper calyx lobe, apex of the lower lip emarginate; lamina of photosynthetic organs with conspicuous nerves and an acute or acuminate apex ---------- 9. *U. praetermissa*
gg. Apex of corolla spur not deflexed, the upper lip about twice as wide as the upper calyx lobe, apex of the lower lip entire; lamina of photosynthetic organs with inconspicuous nerves and an obtuse or subacute apex ---------- 1. *U. alpina*
cc. Terrestrial herbs, with photosynthetic organs usually inconspicuous or absent at anthesis; tubers never present at the base of the inflorescence; corolla mauve or yellow.
h. Corolla violet or white, the lower lip distinctly 3-lobed; photosynthetic organs small, spatulate, rosulate at the base of the inflorescence ---------- 2. *U. amethystina*
hh. Corolla yellow, the lower lip entire; photosynthetic organs linear, thalloid, often absent at anthesis ---------- 7. *U. lloydii*
bb. Bracteoles absent, bract medifixed; corolla yellow.
i. All bracts on the inflorescence axis subtending flowers; corolla spur about as long as the lower lip; lower calyx lobe shorter than the capsule ---------- 11. *U. subulata*
ii. Only the alternate bracts on the inflorescence axis subtending flowers; corolla spur about twice as long as the lower lip; lower calyx lobe exceeding the capsule ---------- 10. *U. pusilla*
aa. Aquatic herbs; photosynthetic organs dissected into capillary segments, always present and conspicuous at anthesis; bracteoles absent, bracts always basifixed.
j. Corolla red; lowermost flower at or near the base of the peduncle; fruiting pedicels sharply reflexed; capsule circumscissile; seeds not winged ---------- 5. *U. hydrocarpa*
jj. Corolla yellow; lowermost flower above the middle of the peduncle; fruiting pedicels erect or recurved; capsule valvate or indehiscent; seeds winged.
k. Flowers numerous (10–20); fruiting pedicels strongly recurved; capsules indehiscent; seeds circular with an inconspicuous hilum and a narrow membranous wing ---------- 4. *U. foliosa*
kk. Flowers few (1–4); fruiting pedicels spreading; capsules laterally bivalvate; seeds with a conspicuous hilum and an irregular corky wing ---------- 8. *U. obtusa*

1. **Utricularia alpina** Jacq., Enum. Pl. Carib. 11. 1760. TYPE: not seen.—FIG. 4.

U. montana Jacq., Sel. Stirp. Amer. 7, *tab.* 6. 1763. Based on *U. alpina* Jacq.
U. grandiflora Pers., Syn. Pl. 1: 18. 1805, nom. illeg., *U. montana* Jacq. cited as synonym.

Perennial epiphytic *herbs*; stolons filiform or slightly fleshy, radiating from the base of the inflorescence, several of them swollen at or near the point of origin and elsewhere to form ellipsoid tubers 1.5–2.0 cm long. *Photosynthetic organs*



FIGURES 2–5. *Utricularia*.—2. *U. unifolia* Ruiz & Pavón.—3. *U. praetermissa* P. Taylor.—4. *U. alpina* Jacq.—5. *U. endresii* Reichenbach f. a = Photosynthetic organ (×1). b = Bract and bracteole (×10). c = Calyx (×1). d = Corolla (×1). [After a variety of tropical American material.]

leaflike, 1–2 from the inflorescence base, 6–25 cm total length; lamina narrowly obovate-elliptic or elliptic, the apex obtuse to subacute, coriaceous, multinerved, the nerves not drying prominent, the base ± strongly decurrent; pseudopetiole usually shorter than the lamina. *Traps* borne on filiform stolon branches, ovoid, stalked, ca. 1 mm long, the mouth basal, the upper lip with 2 subulate recurved appendages. *Inflorescences* 10–35 cm long; peduncle 1–2 mm thick, 1–3-flowered; bracts linear-lanceolate, acute or acuminate, 5–7 mm long, the bracteoles similar but usually narrower and slightly shorter, the sterile scales on the peduncle 2–4, similar to the bracts but shorter; pedicels erect, 4–6 times as long as the bract. *Flowers* with the calyx lobes subequal, ovate, obtuse, basally rounded to subcordate, 2–3 cm long, 1.2–2.0 cm wide; corolla usually white with a yellow palate, 4–6 cm long, glabrous or minutely papillose, especially at the spur apex, the upper lip transversely oblong, apically rounded, 2–3 times as wide, as long as or longer than the upper calyx lobe, the lower lip larger, to 5 cm wide, fan shaped, the apex rounded, entire, the palate gibbous, prominent, the spur subulate, acute, curved upwards, about as long as the lower lip. *Capsules* ovoid, ca. 10 mm long, relatively thick walled, dehiscing by a single abaxial longitudinal slit; seeds numerous, narrowly cylindrical-fusiform, 0.35–0.5 mm long.

This species occurs in Nicaragua, Panama, Colombia, Venezuela, Guyana, Surinam, and the West Indies.

Utricularia alpina is closely allied to *U. endresii*, *U. jamesoniana*, *U. praetermissa*, and *U. unifolia*. All these closely allied species are poorly collected in Panama and the material is incomplete. In Panama and Colombia hybridization may occur. This can perhaps be resolved by careful field study. The specimen seen and cited here as *U. alpina* lacks a corolla and may possibly be *U. praetermissa*. *Utricularia alpina* does occur in Nicaragua so its presence in Panama is possible. It is the only species within the group extending into northeastern South America and the West Indies.

PANAMÁ: Cerro Jefe, 1000 m, *Correa et al. 1626* (MO).

2. **Utricularia amethystina** St.-Hilaire & Girard, Ann. Sci. Nat. Bot., sér. 2, 11: 163. 1839. TYPE: Brazil, Bahia, *Salzmann* (P, holotype; G, K, LE, MO, R, W, isotypes).

Perennial or probably sometimes annual, terrestrial *herbs*; stolons subterranean, trap-bearing, filiform, radiating from the base of the inflorescence. *Photosynthetic organs* usually present at anthesis, 1–3 or more, rosulate at the inflorescence base, reniform or orbicular to narrowly obovate, pseudopetiolate, 0.5–3 cm long. *Traps* ± globose, long stalked, ca. 1 mm in diam., mouth basal, the upper lip with 2 short straight subulate appendages, these and the lower lip with dense incurved gland-tipped hairs. *Inflorescences* 5–30 cm long, 1–6-flowered; bracts ovate-deltoid, acute, 1-nerved, ca. 1 mm long, the bracteoles linear, acute, narrower and somewhat shorter than the bracts, often but not always connate with them for a small to a large part of their length, the bracts thus appearing to be tridentate and without bracteoles, the sterile scales on the peduncle

2–many, similar to the bracts but smaller; pedicels erect or ascending, usually ca. 1 cm long but often shorter or much longer. *Flowers* with the calyx lobes unequal, the upper lobe ovate-oblong, obtuse, 2–3 mm long, strongly cucullate, firm in texture with a narrow more membranous margin, the lower lobe slightly shorter, oblong, less cucullate and of a ± uniform membranous texture; corolla usually violet, mauve or sometimes white with a yellow palate, typically 6–12 mm long but sometimes smaller or larger, the upper lip broadly ovate-oblong, about twice as long as the upper calyx lobe, the lower lip about the same length but broader and ± deeply and equally 3-lobed, the palate gibbous, prominent, the spur narrowly cylindrical or subulate from a conical base, the apex usually obtuse, usually 2–3 times as long as the lower lip. *Capsules* globose, ca. 2 mm in diam., firm in texture, dehiscing by two lateral longitudinal slits into dorsal and ventral valves; seeds numerous, ± ellipsoid, ca. 0.3 mm long.

This species ranges from tropical Florida to Brazil.

COCLÉ: El Valle, 600–1000 m, *Allen 1150* (MO). PANAMÁ: Bald savannalike areas along road toward top of Cerro Campana, *Duke 5954* (MO).

3. **Utricularia endresii** Reichenbach f., Gard. Chron., n.s., 2: 582. 1874. TYPE: Costa Rica, *Endress*, cult. *Veitch* (W, holotype; K, isotype).—FIG. 5.

U. alpina sensu P. Taylor, Mem. New York Bot. Gard. 17: 210. 1967, pro parte, non Jacq.

Perennial epiphytic *herbs*; stolons filiform, radiating from the base of the inflorescence, several swollen at or near the point of origin to form narrowly ellipsoid or fusiform tubers ca. 1 cm long. *Photosynthetic organs* leaflike, 1–3 from the inflorescence base, 6–20 cm total length; lamina membranous, multinerved, narrowly oblanceolate to linear-lanceolate, the apex obtuse to acute; pseudopetiole usually much shorter than the lamina. *Traps* borne on filiform stolon-branches, ovoid, stalked, ca. 1 mm long, the mouth basal, the upper lip with 2 subulate recurved appendages. *Inflorescences* 15–40 cm long; peduncle 1–1.5 mm thick, 1–3-flowered; bracts linear-lanceolate, acute, straight, 5–10 mm long, the bracteoles similar but shorter, the sterile scales on the peduncle 2–4, similar to the bracts but usually shorter; pedicels erect, 3–5 times as long as the bract. *Flowers* with the calyx lobes subequal, ovate, apically rounded or obtuse, 1.5–2.2 cm long, 1.0–1.4 cm wide; corolla violet or mauve with a yellow palate, 3–5 cm long, densely stipitate-glandular, the upper lip orbicular, about twice as wide as the upper calyx lobe, the lower lip much larger, fan shaped, the apex distinctly 3-crenate, the palate gibbous, prominent, the spur narrowly conical-subulate, curved, the apex acute, shorter than the lower lip. *Capsules* and seeds not seen.

This species has been collected in Costa Rica, Panama, Colombia, and Ecuador.

The Chiriquí Volcán and the Seemann specimens cited are undoubtedly *U. endresii* but the latter may not have been collected in what is now Panama. The other three recently collected specimens cited are too incomplete for certain determination.

Utricularia endresii is distinguished from *U. alpina*, *U. praetermissa*, and *U.*

unifolia by its densely stipitate-glandular corolla which is apparently always violet or mauve, its tricrenate lower lip, and its membranous photosynthetic organs.

CHIRIQUÍ: Chiriquí Volcán, collector unknown (W). DARIÉN: Bay of Choco, *Seemann 1112* (BM, K). PANAMÁ: Cerro Jefe, 1000 m, *Gentry 6175* (MO). Near Cerro Campana, *Kirkbride 331* (MO). Cerro Jefe, new road leading N of summit, *Witherspoon & Witherspoon 8534* (K, MO).

4. **Utricularia foliosa** L., Sp. Pl. 18. 1753. LECTOTYPE: Plumier's drawing, Pl. Amer. Fasc. Prim. 7. 158, *tab. 165.* 1758.

Utricularia mixta Barnh., Mem. Torrey Bot. Club 16: 111. 1920. TYPE: Cuba, Isle of Pines, Vivijagua, *Britton et al. 15014* (NY).

Perennial, freely suspended aquatic *herbs*; stolons robust, to several meters long, distinctly flattened, to 4 mm wide, mucilaginous, the internodes 2–15 cm long. *Photosynthetic organs* large and conspicuous, alternate on the stolons, broadly ovate in outline, to 15 cm long, ± dimorphic, some bearing numerous traps, others bearing few or none, repeatedly pinnately dissected into capillary ± terete segments, the ultimate segments setulose. *Traps* lateral on the segments, obliquely ovoid, 1–2 mm long, shortly stalked, the mouth lateral, the upper lip with 2 simple or sparsely branched setiform appendages. *Inflorescences* erect, emergent, 7–45 cm long, usually 10–20-flowered, initially congested, the inflorescence axis elongating with age; peduncle straight, terete, 1–3 mm thick; bracts basifixed, broadly ovate or orbicular, 2–4 mm long, the sterile scales absent or 1–2 just below the lowermost flower; pedicels at first erect, spreading and eventually ± strongly recurved in fruit, to 16 mm long. *Flowers* with the calyx lobes subequal, broadly ovate, 3–4 mm long, ± connate at the base, scarcely accrescent; corolla yellow, 8–15 mm long, the upper lip ± orbicular, the lower lip larger, oblate to subreniform, the apex rounded, entire or emarginate, the palate much raised and spurred, the spur narrowly conical, as long as or slightly shorter than the lower lip. *Capsules* globose, to 8 mm in diam., indehiscent, becoming detached and floating when ripe; seeds few, lenticular, 2–2.5 mm in diam. with a narrow regular hyaline wing.

This species is distributed from the southeastern United States to Argentina and the Galapagos Islands, and in tropical Africa and Madagascar.

CANAL ZONE: Barro Colorado Island, *Aviles 906* (F); *Starry 80* (F); *Shattuck 369* (LIL, MO). Gamboa, Río Chagres, *Allen 1975* (MO). Gatún Lake, *Dodge 16769* (G, MO). Gigante Bay, *Dodge 3470* (NY). Between Frijoles and Monte Lirio, *Killip 12180* (NY). Gamboa, *Lazor & Boreham 2930* (FSU, MO). Darién Station, *Standley 31562* (NY), *31646* (US). Madden Lake, *Woodson & Schery 961* (MO, NY). PANAMÁ: Juan Mina, Río Aguardiente Chico, *Bartlett & Lasser 16496* (MO). Río Pescodo, SE part of Gatún Lake, *Bartlett & Lasser 16601, 16606* (both MO).

5. **Utricularia hydrocarpa** Vahl, Enum. Pl. 1: 200. 1804. TYPE: Guyana ("Cajenna"), *Richard* (C, holotype; P, isotype).

Perennial, freely suspended aquatic *herbs*; stolons filiform, terete, to 30 cm long or longer, 0.5–1.5 mm thick. *Photosynthetic organs* conspicuous, alternate on

the stolons, 1.5–3.0 cm long, repeatedly dichotomously divided into capillary segments, the ultimate segments sparsely setulose. *Traps* lateral on the segments, oblique, broadly ovoid, 1–2 mm long, short stalked, the mouth lateral, naked or with 2 short simple setiform appendages. *Inflorescences* erect, emergent, 3–10 cm long, the 3–6 flowers widely spaced on the axis, the lowermost flower cleistogamous, at or very near the base of the peduncle; bracts basifixed, broadly ovate-deltoid, auriculate, 2–3 mm long, the sterile scales absent; pedicels at first erect becoming sharply reflexed in fruit. *Flowers* with the calyx lobes subequal, broadly ovate, the apex of the upper lobe obtuse, that of the lower lobe deeply emarginate; corolla red or pink, ca. 8 mm long, the upper lip orbicular, the apex entire, 4–5 mm wide, the lower lip transversely oblong, the apex emarginate, 6–8 mm wide, the palate slightly gibbous, the spur conical-subulate, obtuse, shorter than the lower lip. *Capsules* globose, ca. 3 mm in diam. with a persistent style 1–1.5 mm long, circumscissile; seeds depressed globose, ca. 0.5 mm in diam., finely reticulate.

This species ranges from Cuba and Belize to Bolivia and Brazil.

CANAL ZONE: Juan Mina, *Bartlett & Lasser 16410, 16710* (both MO). COCLÉ: *Pittier 4834* (NY, US). PANAMÁ: Between Panama and Chepo, *Dodge et al. 16716* (MO). Near Chepo, *Pittier 4554* (NY, US). Matías Hernández, *Pittier 6893* (G, US). Bejuco, *Woodson et al. 1684* (MO, NY).

6. **Utricularia jamesoniana** Oliver, J. Proc. Linn. Soc., Bot. 4: 169, *tab. 1, fig. 1.* 1860; P. Taylor, Opera Bot., Ser. B, 4: 15, *fig. 1B.* 1975. TYPE: Ecuador, Cosanga River, *Jameson 1* (K, holotype).

Perennial epiphytic *herbs*; trap-bearing filiform stolons radiating from the base of the inflorescence, several swollen near the point of origin into fusiform tubers to 6 mm long and 2–3 mm thick. *Photosynthetic organs* leaflike, 2–3 from the inflorescence base, obovate-spatulate to elliptic, 1–2 cm (total length); lamina 2–4 mm wide, multinerved, membranous; pseudopetiole shorter than the lamina. *Traps* globose, stalked, ca. 0.7 mm long, the mouth basal, the upper lip with 2 subulate recurved appendages. *Inflorescences* 2–10 cm long, 1–3-flowered; bracts narrowly elliptic, 4–7 mm long, the bracteoles similar or narrower, the sterile scales on the peduncle usually only one, subulate, smaller than the bracts; pedicels erect, 5–10 mm long. *Flowers* with the calyx lobes subequal, broadly ovate, basally truncate or subcordate, the apex rounded, 4–12 mm long; corolla 10–20 mm long, white, more or less tinged with violet, lavender, or lilac and sometimes marked with yellow on the palate, the outer surface, especially the margins of the lobes and apical half of the spur, densely stipitate-glandular, the upper lip ± orbicular, ± 4-crenate, slightly longer and wider than the upper calyx lobe, the apex rounded or emarginate, the lower lip a little longer, ± deeply 3-lobed, the palate scarcely prominent, the spur 2–4 times as long as the lower lip, narrowly conical in its basal half, subulate and curved or abruptly bent upwards in its

apical half. *Capsules* ovoid, ca. 4 mm long; seeds numerous, narrowly cylindrical, ca. 0.3 mm long.

This species occurs from Guatemala to Peru, Guyana, and the West Indies.

Utricularia jamesoniana is very variable in flower size. Specimens exist, e.g. *Correa & Dressler 1045*, which have every appearance of being hybrids between this and one of the other epiphytic species. Field observation is highly desirable. From Ecuador and Colombia a closely related species with larger corolla lobes and photosynthetic organs has recently been described as *U. asplundii* P. Taylor (Taylor, 1975: 16). It may possibly extend into Panama.

DARIÉN: Top of W ridge of Cerro Tacarcuna, 1800–1850 m, *Gentry & Mori 14026* (MO). PANAMÁ: Cerro Jefe, 2.5 mi beyond Finca Indio, *Gentry 2140* (MO). Cerro Jefe, 1000 m, *Luteyn & Kennedy 1777* (DUKE). Along Río Piedras ca. 25 km NE of Cerro Azul, 550 m, *Mori & Kallunki 3349* (MO).

7. **Utricularia lloydii** Merl, Bull. Torrey Bot. Club 61: 367. 1934. TYPE: Brazil, Rio Branco, Retiro do Serra da Lira, *Geraldo* (NY, holotype; M, isotype).

Annual or perhaps perennial terrestrial *herbs*; subterranean trap-bearing capillary stolons radiating from the base of the inflorescence. *Photosynthetic organs* arising from the stolons, narrowly linear, thalloid, 1-nerved, to 0.6 mm wide, delicate and apparently usually ± decayed at anthesis. *Traps* sessile on the stolons and photosynthetic organs, less than 1 mm long, dimorphic, some globose, the mouth basal, the upper lip with 2 deltoid appendages, the lower lip with a single shorter rounded appendage, all appendages densely covered with gland-tipped hairs, the other traps ovoid, the mouth ± lateral, the upper lip with 2 subulate appendages and a few sessile glands, the lower lip with a single longer rounded appendage, glabrous. *Inflorescences* 3–17 cm long, 1–5-flowered; bracts ovate, acute or acuminate, 1.5–2 mm long, the bracteoles subulate, less than 1 mm long, the sterile scales on the peduncle 1–4, similar to the bracts; pedicels erect at anthesis, spreading in fruit, 2–4 mm long. *Flowers* with the calyx lobes ovate, membranous, obscurely nerved, the upper lobe 3–4 mm long, the apex obtuse or acute, the lower lobe slightly longer, the apex obscurely bidentate; corolla yellow, 6–7 mm long, the upper lip ovate-oblong, slightly longer and wider than the upper calyx lobe, the lower lip ± orbicular, longer than the upper lip, the palate prominent, the spur subulate, acute, 1.5–2 times as long as the lower lip. *Capsules* ± globose, dorsiventrally compressed, ca. 2.5 mm in diam., the walls membranous, narrowly thickened on either side of the longitudinal abaxial suture; seeds globose, ca. 0.25 mm in diam., reticulate, the areolae few and relatively large, ¼–⅓ the seed diam.

This species has been collected in Panama, Surinam, and Brazil, and is probably overlooked elsewhere in South America.

Apparently only the US sheet of this number includes specimens of *U. lloydii*; the sheet at K and F are entirely *U. subulata*.

COCLÉ: Penonomé, llanos outside of town, *Ebinger 1014* (US, in part, mixed with *U. subulata*).

8. **Utricularia obtusa** Swartz, Prodr. Veg. Ind. Occ. 14. 1788. TYPE: Jamaica, *Swartz s.n.* (S, holotype; BM, C, G, LD, M, isotypes).

U. gibba sensu P. Taylor, Kew Bull. 18: 197. 1964, pro parte, non L., Sp. Pl. 18. 1753.

Perennial *herbs*, freely suspended or more commonly affixed; stolons fasciculate from the peduncle base, filiform, terete, to 20 cm long, ca. 1 mm thick, often mat-forming. *Photosynthetic organs* numerous, alternate on the stolons, to 2 cm long, sparsely dichotomously dissected into 2–6 capillary segments. *Traps* lateral on the segments, obliquely ovoid, 1–1.5 mm long, short stalked, the mouth lateral with the marginal simple setae, the upper lip with 2 usually long, ± branched setiform appendages. *Inflorescences* erect, emergent, variable in length but mostly 5–10 cm long, 2–6-flowered; peduncle terete, usually less than 1 mm thick; bracts basifixed, broadly ovate, obtuse, ca. 1 mm long, the sterile scales on the peduncle 1 or 2, remote from lowermost flower; pedicels erect at anthesis, spreading in fruit, 5–15 mm long. *Flowers* with the calyx lobes similar, ± ovate, 2–3 mm long; corolla yellow with orange or brownish marks on the palate, variable in size but mostly 10–15 mm long, the upper lip broadly ovate or ± orbicular, obscurely 3-crenate, the lower lip usually slightly smaller, ± orbicular, entire, the palate spurred, prominent, the spur ± subulate from a conical base, straight or ± curved, the apex obtuse or minutely bifid, about as long as the lower lip. *Capsules* globose, 2–4 mm in diam. dehiscing into 2 lateral valves; seeds lenticular, ca. 1 mm wide with a pronounced hilum and an irregular corky wing.

This species occurs in Central and South America and in tropical Africa.

CANAL ZONE: Juan Mina, *Bartlett & Lasser 16409* (MO). Barro Colorado Island, *Croat 5649, 13985, 14104* (all MO). Lion Hill Sta., P.R.R., *Hayes 698* (K). Chagres River upstream of Gamboa, *Lazor & Boreham 2920* (FSU, MO). Chagres River N of Gamboa, *Lazor et al. 3738* (DUKE, FSU, MO, US). Summit Gardens, *Porter et al. 5177* (MO).

9. **Utricularia praetermissa** P. Taylor.[3] TYPE: Costa Rica, Prov. San José, La Palma, 1550 m, Aug. 1898 *Tonduz 12471* (K, holotype; BM, F, G, M, MO, US, W, isotypes).—FIG. 3.

Perennial epiphytic *herbs*; stolons branched, filiform, radiating from the base of the inflorescence, several swollen at or near the point of origin to form ellipsoid tubers 1–2 cm long. *Photosynthetic organs* 2–4 from the inflorescence base, leaflike, 8–15 cm long; lamina coriaceous, multinerved, the nerves drying prominent on both surfaces, narrowly elliptic, the apex acute or acuminate; pseudopetiole usually as long as or longer than the lamina. *Traps* borne on filiform stolon-branches, ovoid, stalked, ca. 1 mm long, the mouth basal, the upper lip with 2 subulate recurved appendages. *Inflorescences* to 30 cm long; peduncle 1.5–2 mm thick, 1–3-flowered; bracts linear-lanceolate, acute or acuminate, straight, 5–7 mm long, the bracteoles similar but narrower and sometimes shorter, the sterile scales on the peduncle usually ca. 4, similar to the bracts but usually smaller; pedicels erect, 2–4 times as long as bract. *Flowers* with the calyx lobes

[3] *Utricularia praetermissa* P. Taylor, sp. nov. Species affinis *U. unifolia* Ruiz & Pavón sed bracteis multo brevioribus et corolla calcari longiore apice deflexo satis differt.

subequal, ovate, ± obtusely acuminate, 2.5–3 cm long, 1.2–1.5 cm wide; corolla white or mauve with a yellow palate, 4–5 cm long, glabrous or with a few stipitate glands, the upper lip broadly ovate to orbicular, a little shorter and wider than the upper calyx lobe, the lower lip much larger, transversely elliptic or almost orbicular, to 5 cm wide, apically retuse, the palate gibbous, prominent, the spur narrowly cylindrical, about as long as lower lip, curved upwards, abruptly terminating in an acute subulate deflexed apex. *Capsules* ± globose, ca. 1 cm long; seeds numerous, narrowly cylindrical-fusiform, ca. 0.8 mm long.

This species occurs in Costa Rica, Nicaragua, Panama, and probably Colombia.

The identification of *Utricularia praetermissa*, which is closely allied to *U. unifolia* and *U. alpina*, is not difficult with reasonably complete material. From *U. unifolia* it differs in its much shorter straight bracts and bracteoles, its deflexed spur apex, and its relatively short pseudopetiole. From *U. alpina* it may be distinguished by spur apex, the shape of the lower lip, and the shape and venation of the photosynthetic organs. Within this group of large-flowered epiphytic *Utricularia* species there is one other (to be described shortly) which apparently occurs only in a restricted area in northern Venezuela. Its corolla is similar in shape to that of *U. praetermissa* but is smaller. This is a much smaller plant with very small photosynthetic organs, only a centimeter or two long.

COCLÉ: N of El Valle de Antón, trail to Las Minas, 1000 m, *Allen 2704* (US), *3602* (MO). PANAMÁ: Cerro Jefe, 3000 ft, *Correa & Gauger 193* (DUKE). Cerro Jefe, 2900 ft, *Dwyer & Hayden 8081* (MO). Cerro Campana, *Luteyn & Kennedy 1783* (DUKE). Cerro Jefe, ca. 1000 m, *Mori 7113* (MO).

10. **Utricularia pusilla** Vahl, Enum. Pl. 1: 202. 1804. Guyana ("Cajenna"), *Richard* (C, holotype; G, P, isotypes).

Annual or perhaps sometimes perennial terrestrial *herbs;* stolons filiform, subterranean, bearing photosynthetic organs and traps. *Photosynthetic organs* obovate-spatulate, 1-nerved, sometimes numerous and conspicuous but often ± decayed at anthesis, to 10 mm long and 3 mm wide. *Traps* obliquely ovoid, stalked, ca. 0.5 mm long, the mouth lateral, the upper lip with 2 subulate densely ciliate appendages. *Inflorescences* to 7 cm long; peduncle filiform, 1–15-flowered; bracts peltate, ± orbicular, the sterile scales similar to the bracts, numerous on the peduncle below the raceme and also alternating with fertile bracts on the raceme axis; pedicels spreading, 1.5–2.5 mm long. *Flowers* with the calyx lobes ovate, unequal, the lower lobe slightly larger; corolla yellow, ca. 6 mm long, the upper lip narrowly ovate, entire, the lower lip descending, 3-lobed, the palate gibbous, the spur subulate, acute, descending, 2–3 times as long as the lower lip. *Capsules* globose, ca. 1.5 mm long, considerably exceeded by the accrescent lower lobe of the calyx; seeds ovoid, ca. 0.35 mm long with about 11 longitudinal striations.

This species ranges from Mexico to Argentina.

CANAL ZONE: Fort Kobbe, *Duke & Mussell 6571* (K, MO). CHIRIQUÍ: Boquete, 3800 ft, *Davidson 659* (F, NY, US). Alto Boquete, *Partch 69-125* (MO). COCLÉ: El Valle de Antón, 2000 ft, *Dwyer et al. 7935* (K, MO). 3–4 mi above El Valle, *Gentry & Dwyer 3687* (MO).

El Valle de Antón, 1000 m, *Luteyn 1168* (DUKE); *Miller 1821* (US). 3 km N of El Valle, *Mori & Kallunki 2965* (MO). La Mesa, 4 km N of El Valle, 875 m, *Nee & Dwyer 9202* (MO). Aguadulce, *Pittier 4944* (NY, US). La Mesa, 5 mi N of El Valle, 2500 ft, *Tyson et al. 2471* (FSU). Inside the crater of El Valle de Antón, 1000 m, *Wilbur et al. 11137* (DUKE). Penonomé, *Williams 161* (NY). Near Antón, *Woodson et al. 1713* (GH, NA, NY). PANAMÁ: Between Capira and Potrero, 80–130 m, *Dodge & Hunter 8614* (G). N of Panama City, *Paul 570* (US). Panama City, *Seemann 263* (BM, K). Between Pacora and Chepo, 25 m, *Woodson et al. 1656* (NA, NY).

11. **Utricularia subulata** L., Sp. Pl. 18. 1753. TYPE: Virginia, *Clayton* (BM, holotype).

Annual or perhaps perennial terrestrial *herbs*; stolons capillary, subterranean, bearing a photosynthetic organ and traps. *Photosynthetic organs* narrowly linear, 1-nerved, sometimes numerous and conspicuous but often ± decayed at anthesis, to 20 mm long and 0.5 mm wide. *Traps* obliquely ovoid, stalked, 0.2–0.5 mm long, the mouth lateral, the upper lip with 2 subulate sparsely branched appendages. *Inflorescences* to 25 cm long; peduncle capillary, 1–25-flowered; bracts peltate, orbicular to elliptic, the sterile scales numerous on the peduncle below the raceme; pedicels ascending, 2–10 mm long. *Flowers* with the calyx lobes ± ovate, subequal; corolla yellow, usually 6–10 mm long but much reduced in cleistogamous flowers, the upper lip broadly ovate, entire, the lower lip deeply 3-lobed, the palate conspicuously bigibbous, the spur subulate, obtuse, descending, about as long as the lower lip. *Capsules* globose, ca. 1.5 mm long, dehiscing by an abaxial ovate pore; seeds ovoid, ca. 0.25 mm long with ca. 15 longitudinal striations.

This species is distributed from eastern North America to Argentina, Portugal, tropical and South Africa, Madagascar, Thailand, Malaya, and Borneo.

Perhaps the commonest of all *Utricularia* species, *U. subulata* may be more frequent and widespread in Panama than indicated by the collections. It is as conspicuous as *U. pusilla*, which is represented by numerous specimens.

Gibson (1974: 328) implied that *U. subulata* and *U. pusilla* are not two distinct species, but the two are different. The sterile bracts on the inflorescence axis of *U. pusilla* are diagnostic; in addition the corolla, calyx, seeds, traps, and photosynthetic organs are significantly and constantly different in the two species.

COCLÉ: Penonomé, llanos outside of town, *Ebinger 1014* (F, K, US—in part). PANAMÁ: E side of Cerro Campana, 600–650 m, *Nee 6847* (K, MO).

12. **Utricularia unifolia** Ruiz & Pavón, Fl. Peruv. Chil. 1: 20, *tab. 31b.* 1798. TYPE: not seen.—FIG. 2.

U. alpina sensu P. Taylor, Mem. New York Bot. Gard. 17: 210. 1967, pro parte, non Jacq.

Perennial epiphytic *herbs*; stolons fleshy, radiating from the base of the inflorescence, several swollen near the point of origin to form ellipsoid tubers 1–1.5 cm long. *Photosynthetic organs* 1–4, leaflike, 5–15 cm long; lamina coriaceous, multinerved, the nerves drying prominent on both surfaces, narrowly elliptic to elliptic, to 2.5 cm wide, the apex acute or acuminate; pseudopetiole usually 2–3 or more times as long as the lamina. *Traps* borne on filiform stolon-branches,

ovoid, stalked, ca. 1 mm long, the mouth basal, the upper lip with 2 subulate recurved appendages. *Inflorescences* to 30 cm long; peduncle 1.5–2 mm thick, 1–3-flowered; bracts linear-lanceolate, acute, usually falcate, 1–3 cm long, the bracteoles similar but much narrower and shorter, the sterile scales on the peduncle 2–4, similar to the bracts and often larger; pedicels erect, 1–3 times as long as the bract. *Flowers* with the calyx lobes subequal, ovate, acute, 2–4 cm long, 1.3–2.0 cm wide; corolla violet or mauve with a yellow palate, 3–5 cm long, glabrous or sparsely stipitate-glandular, the upper lip broadly ovate to ± orbicular, the apex rounded, about as wide as the upper calyx lobe, the lower lip much larger, transversely elliptic, apically retuse or emarginate, the palate gibbous, prominent, the spur narrowly conical-subulate, curved, the apex obtuse or subacute, shorter than the lower lip. *Capsules* ± globose, 8–12 mm long; seeds numerous, narrowly cylindrical-fusiform, 0.35–0.5 mm long.

This species occurs in Costa Rica, Panama, Colombia, Ecuador, Peru, and Bolivia.

Utricularia unifolia is distinguished from related species by its relatively long, often curved bracts. It is the only species in the group ranging southward into the Andes of Peru and Bolivia.

CHIRIQUÍ: Boquete Trail, Cerro Respinga, E of town of Cerro Punta, 2000–2500 ft, *Gentry 5925* (MO). DARIÉN: Cerro Pirre, 2500–4500 ft, *Duke & Elias 13735* (MO).

13. U. sp.

? Perennial terrestrial *herbs*; a few trap-bearing filiform stolons radiating from the base of the inflorescence. *Photosynthetic organs* 3, rosulate at the inflorescence base, narrowly obovate-spatulate, to 35 mm long, ca. 2 mm wide near the apex, obscurely multinerved. *Traps* apparently obliquely ovoid, ca. 1 mm long, stalked, the mouth basal, the upper lip with 2 subulate appendages sparsely beset with sessile and stalked glands, the lower lip with a few stalked glands. *Inflorescence* apparently ca. 5 cm long, 1–2-flowered; bract subulate, ca. 1 mm long, the bracteoles apparently absent, the sterile scales on the peduncle 2, similar to the bract; pedicel ca. 10 mm long, apparently erect. *Flowers* with the calyx lobes similar, the upper lobe ovate, ca. 2 mm long, the lower lobe shorter, almost orbicular (the apex perhaps missing); corolla ca. 10 mm long, the upper lip shape not determined, the lower lip apparently transversely oblong, perhaps 9 mm wide, the spur apparently subulate, about as long as the lower lip. *Fruits* not seen.

The specimen cited and described above is too incomplete for determination but is clearly not referable to any of the 12 preceding species. It resembles most closely *U. hispida* Lam. which occurs in Guatemala, Honduras, and in much of northern South America. The traps, calyx and what can be seen of the corolla are similar. However, that species normally has a long, multiflowered inflorescence and much longer photosynthetic organs, and it usually grows in low-altitude savanna.

PANAMÁ: Cerro Trinidad, on wet rock faces of main peak, 800–1000 m, (in flower) 20 Oct. 1946, *Allen 3767* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 181. VALERIANACEAE

FREDERICK G. MEYER[2]

Annual or perennial *herbs*, or rarely *shrubs*, mostly erect, sometimes clambering, rarely voluble, occasionally caespitose, characteristically foetid when dry, unarmed, glabrous or with simple hairs, with creeping rhizomes or taproots, sometimes subnapiform and turniplike, the stems usually fistulose, subscapose or leafy, terete or occasionally more or less quadrangular. *Leaves* opposite, simple or compound, often imparipinnate, rarely ternate, cauline, sometimes strongly crowded and thickened, or basal, occasionally forming a dense cushion "polster," the leaves and leaflets entire to variously serrate, dentate or incised to pinnatisect, membranous to subcarnose or subcoriaceous, the bases often sheathing, glabrous or when pubescent the hairs short, glands and stipules absent; leaflets sessile or short-petiolulate. *Inflorescences* determinate, thyrsoid or cymose, many- or rarely few-flowered, terminal and axillary, more or less pyramidal, open and diffuse to glomerate, sometimes caespitose on a thickened convex cushionlike head, sometimes corymbiform, the cymes more or less flat-topped, the ultimate dichotomies sometimes scorpioid; bracts and bracteoles present, free or sometimes connate and sheathlike. *Flowers* entomophilous, perfect, polygamous, dioecious or polygamodioecious (usually gynodioecious), epigynous, irregular or nearly regular in unisexual flowers, (1–3–)5-merous; calyx epigynous, adnate to the ovary, the limb crateriform, erect to urceolate, toothed, or the segments inrolled at anthesis and later expanded and pappuslike with plumose setae; corolla superior, gamopetalous, infundibuliform to subsalverform, campanulate to rotate, often gibbous or spurred at the base, sometimes bilabiate, white, yellow, or red, the limb 5-lobed, rarely 4–6-lobed, the lobes usually unequal, imbricate in bud, glabrous without, sometimes pilosulous or short-sericeous in the throat; stamens 1–4 by reduction, inserted on the corolla tube, alternate with the corolla lobes, included and sessile or the filaments exserted, the anthers dorsifixed and versatile, usually 2-lobed, introrse, dehiscing longitudinally, the thecae usually somewhat lunate and opposed, sulcate, the locules equal in length or 4-lobed, the ventral locules of each theca slightly longer than the dorsal and essentially parallel; pollen 3-colporate; ovary inferior, 3-locular with 2 locules abaxial and sterile, 1 median, adaxial

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[1] Assisted by National Science Foundation Grant BMS-72-02441 A03 (Thomas B. Croat, principal investigator).

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ANN. MISSOURI BOT. GARD. 63: 581–592. 1976.

and fertile, opposite a bracteole, the ovules 1 per locule and aborting in two locules, pendular from the apex of the locule, anatropous, the style simple, filiform, included or exserted, the stigmas 3, erect or spreading, sometimes papillate. *Fruits* cypselate achenes, rarely adnate to the peduncle and connate, dry and indehiscent, often nutlike, glabrous or pubescent, 1-seeded, adaxial veins 3, 1 median, 2 peripheral, abaxial veins 3, the sterile locules flat, sometimes lobulate or rarely winglike and strongly veined, the adnate calyx limb persistent, coronate, unlobed or variously lobed or setulose and pappuslike; seed with a straight embryo, the endosperm absent. Chromosome numbers, $x = 7, 8, 9, 11$.

Valerianaceae is a family of about 14 genera with about 400 species, distributed in all the continents except Australia. Most species occur in temperate regions or on tropical mountains. Five genera occur in the Old World. The nine New World genera are concentrated largely in South America, where the greatest morphological diversity in the family occurs, including species with a woody and also a cushion-forming habit.

The type genus is *Valeriana*.

As a member of the Rubiales, the Valerianaceae is chiefly an herbaceous group most closely related to the Dipsacaceae. Typically, Valerianaceae are identified by the cymose inflorescence, irregular, often gibbose or spurred pentamerous flowers, a reduction in number of stamens, an ovary with 1 perfect, 1-ovulate locule and often 2 empty locules, and calyx lobes much reduced or sometimes becoming plumose and pappuslike. When dry, many members of the family emit a characteristic pungent odor.

Various members of the family are used medicinally, in particular, species of *Nardostachys* and *Valeriana*. The Panamanian taxa have no known uses.

In Panama, the Valerianceae consists of two genera, *Astrephia*, which is monotypic, and *Valeriana*, with five taxa.

Literature:

Weberling, F. 1961. Die Infloreszenzen der Valerianaceen und ihre systematische Bedeutung. Akad. Wiss. Abh. Math.-Naturwiss. Kl. 1961 (5): 155–281.

a. Achenes adnate to the base of the peduncle, those of the ultimate branches usually connate; inflorescences few-flowered, long-pedunculate; cymes not scorpioid ..... 1. *Astrephia*

aa. Achenes free, axillary in a bract; inflorescences many-flowered; cymes scorpioid ..... 2. *Valeriana*

1. ASTREPHIA

Astrephia Dufresne, Hist. Nat. Méd. Fam. Valérianées 52. 1811. TYPE: *Valeriana chaerophylloides* J. E. Smith.

Annual *herbs*, usually with lithe, diffuse, often clambering branches; stems terete, fistulose. *Leaves* opposite, imparipinnate, petiolate; leaflets incised to laciniate or pinnatifid, petiolulate. *Inflorescences* axillary, cymose, long-pedunculate, corymbose; peduncles strongly ascending, sometimes inflated, adnate to the achenes at the base, 7–15-flowered and bracteate. *Flowers* hermaphroditic

or gynodioecious (rarely), autogamous; calyx limb crateriform; corolla infundibuliform, irregular, gibbous, the lobes subequal, quincunical in bud; stamens inserted on the tube, alternate with the petal limb, the anthers 4-locular, introrse, versatile, 4-lobed, the thecae sulcate, the ventral locules longer than the dorsal and parallel; ovary inferior, basically 3-carpellate, maturing 1 fertile adaxial carpel, the ovule 1, pendulous, anatropous, the style elongate, the stigma lobes 3. *Fruits* cypselate achenes, sessile, pedicellate, usually 2 or 3 together and connate, irregularly obovoid and angled, adnate to the base of the peduncle, more or less corniculate and nutlike, turgid, thick-walled, subspherical to lenticular, the fertile cell larger than the 2 empty cells; seeds compressed.

This is a monotypic, chiefly Andean genus, found in Colombia, Ecuador, and Peru. The first record for Panama was in 1966 from the Chiriquí mountains, the most northerly station known for the plant.

The genus is wholly distinct from other members of the family, primarily by the few-flowered, long-pedunculate inflorescences and the achenes which are connate. The affinities of *Astrephia* appear to be with *Plectritis* and *Valerianella*.

Literature:

Killip, E. P. 1937. Valerianaceae. *In* J. F. Macbride, Flora of Peru. Fieldiana, Bot. Ser. 13: 287–321.

Weberling, F. 1960. Zur systematischen Stellung der Valerianaceengattung *Astrephia* Dufr. Bot. Jahr. Syst. 79: 394–404.

1. **Astrephia chaerophylloides** (J. E. Smith) DC., Prodr. 4: 629. 1830.—Fig. 1.

Valeriana chaerophylloides J. E. Smith, Pl. Icon. Hact. Ined. 3: 53, *tab.* 53. 1791. TYPE: In provincia Chancay Peruae, *Dombey s.n.* (not seen).

Boerhaavia chaerophylloides (J. E. Smith) Willd., Sp. Pl. 1: 22. 1797.

Valeriana laciniata Ruiz & Pavón, Fl. Peruv. Chil. 1: 42, *tab. 69a.* 1798. TYPE: Peru, in collibus Limae et Chancay inter rupes, affatim in nemoribus Chinchao et Muna, *Ruiz & Pavón s.n.* (not seen).

Astrephia laciniata (Ruiz & Pavón) Dufresne, Hist. Nat. Méd. Fam. Valérianées 52. 1811.

Annual *herbs* (0.3–)1.2–12.8 cm tall, sparsely branched or unbranched, mostly glabrous; stems slender, to 6 mm in diameter; internodes widely spaced, 4–10.5 cm apart, often densely squamose, rarely glabrous; roots shallow, fibrous. *Leaves* 6–9(–11)-foliolate, lanceolate to narrowly ovate in outline, spreading to ascending; petioles to 3 cm long; leaflets alternate or opposite, mostly elliptic to broadly elliptic, acuminate, cuneate to truncate at base, 1.4–3.4 cm long, 0.5–2 cm wide, decurrent on the rachis, or the petiolules 1–5 mm long, serrate, biserrate to crenate, pinnatifid or incised to laciniate, often papillate at the insertion with the rachis on the upper side, the terminal lobe sometimes 3-notched, membranous, the main lateral veins extending to the sinuses, the midvein not prominent. *Inflorescences* long-penduculate; peduncles 3.9–5.0 cm long, slender, ascending, the upper side sulcate, pubescent near the base and to the middle of the peduncle; cymes open, 7–14-flowered; bracts of the lowest dichotomy spatulate, often sparsely serrate or papillate, 3–4.5 mm long, progressively smaller above. *Flowers* sessile or pedunculate; calyx limb coronate, obsoletely 5-lobed, often ringed with a crown-

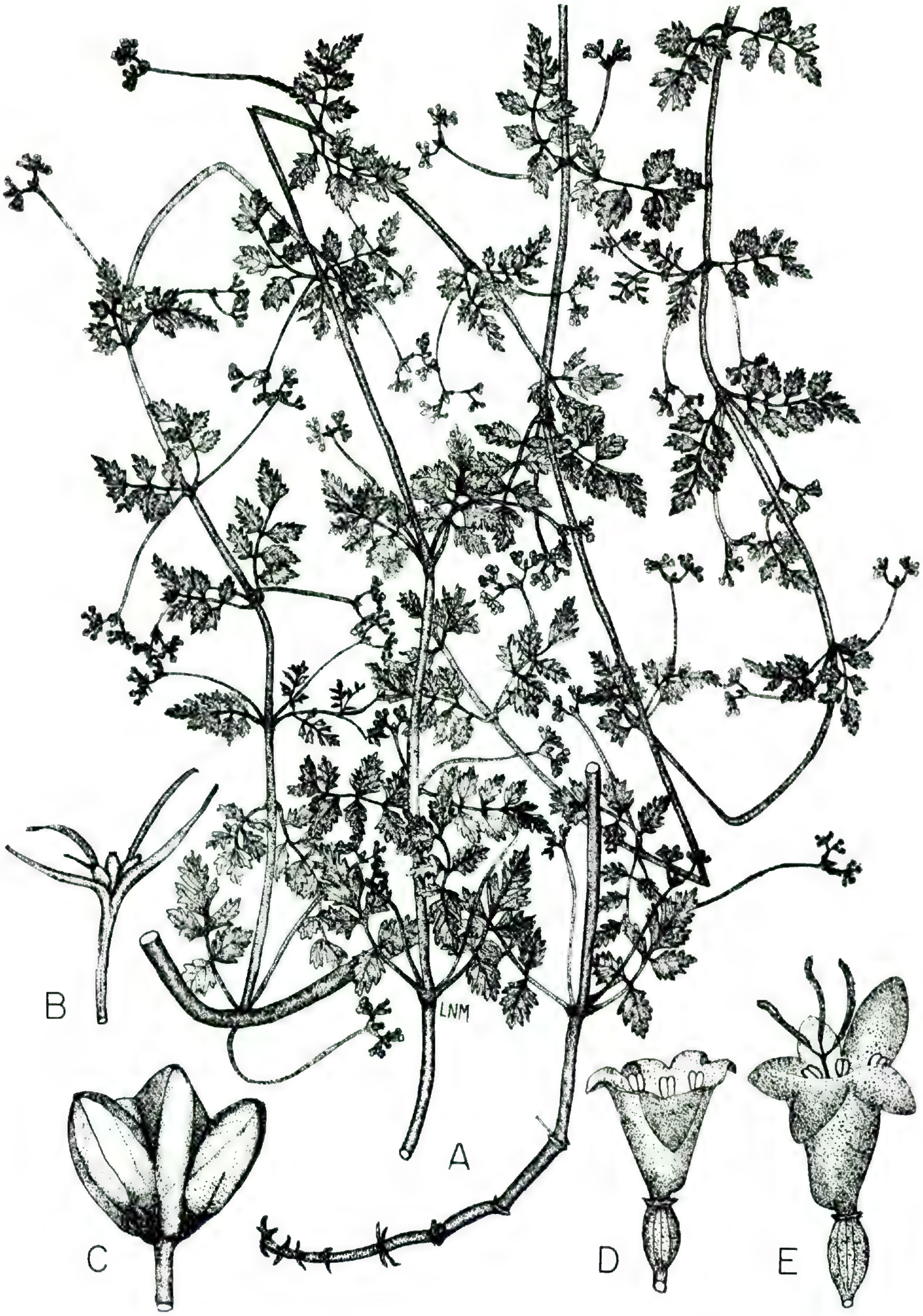


FIGURE 1. *Astrephia chaerophylloides* (J. E. Smith) DC.—A. Habit (×⅖).—B. Young connate achenes (×13).—C. Mature connate achenes (×20).—D. Perfect flower, stigma enclosed (×8½).—E. Pistillate flower, stigmas exserted (×13). [A, D after *Lewis et al. 343* (MO); B, C after *Wilbur et al. 15488* (DUKE); E after *Macbride & Featherstone 191* (US).]

like fringe of 10–15 papillae; corolla white to pinkish, 2–3 mm long (in perfect flowers), 2 mm long (in pistillate flowers), pubescent in the throat or glabrous, the lobes ca. 0.5 mm long, subequal, the posterior lobe largest, acute, rounded to subacute and slightly recurved at the tip; stamens 3, included, the anthers oblong; style and stigmas included (exserted in gynodioecious flowers), glabrous or sometimes papillose, the stigmas papillose and spreading. *Achenes* axillary, papillate-hairy adaxially, especially when young, oblique, usually 1 in the axil of the lowest dichotomy and adnate to the peduncle, in the ultimate dichotomies 2 to 3 together and connate, corniculate and nutlike, or, when borne singly on the ultimate dichotomies, then usually subspherical to lenticular, 2–2.5 mm long, the fertile abaxial locule longer than the 2 empty and smaller abaxial locules; seed 1 in each fertile locule.

The Panamanian material closely resembles specimens from nearby Colombia. This species ranges to Ecuador and Peru. Two races of plants may exist in this taxon in relation to flower size, i.e., plants with small flowers (2 mm long) and plants with larger flowers (3 mm long). Gynodioecism has also been observed in the species.

CHIRIQUÍ: Ca. 6 km WNW of Boquete, 1600 m, *Davidse & D'Arcy 10141* (MO). Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 343* (GH, K, MO, UC, US). Between Alto Quiel and the Río Caldera on the Bajo Chorro Trail, near Finca Lérida, ca. 9 mi NW of Boquete, 1700 m, *Wilbur et al. 15488* (DUKE).

2. VALERIANA

Valeriana L., Sp. Pl. 31. 1753; Gen. Pl., ed. 5. 19. 1754. TYPE: *V. officinalis* L.

Amplophus[3] Raf., Aut. Bot. 89. 1840. Based on *V. scandens* L.

Erect, sometimes voluble or clambering *herbs*, rarely *shrubs*, characteristically foetid when dry, with creeping rhizomes or subnapiform taproots; stems subscapose or leafy, fistulose, terete or occasionally more or less quadrangular. *Leaves* decussate, basal and cauline, spatulate and undivided or pinnate to pinnatifid or rarely bipinnatifid, often imparipinnate, rarely ternate, frequently more or less decurrent on the subpetiolar and more or less clasping-patelliform base, serrate, crenate, dentate, repand or entire, membranous to firm, glabrous or short-pubescent, glands and stipules absent. *Inflorescences* determinate, aggregate-dichasial and thyrsoid or cymose, compound, dense and more or less scorpioid, many-flowered, terminal or sometimes axillary, pyramidal or corymbiform, the cymes more or less flat topped, bracteate and bracteolate. *Flowers* white, rarely yellow, hermaphroditic, gynodioecious or polygamodioecious, epigynous, irregular or nearly regular in unisexual flowers; calyx initially involute, later spreading, the sessile limb concrescent and short-patelliform, hyaline and membranous, becoming setose in mid-plane, the setae plumose, or the limb short-cupuliform and more or less irregularly toothed or lobed; corolla infundibuliform, subcampanulate or rotate, the tube gibbous or straight, usually more or less hairy on the throat, the

[3] This is the only generic synonym applicable for Panamanian material.

5 lobes equal or subequal; stamens 3, rarely 4, adnate on the throat, the anthers essentially sessile and included, or filamentous and exserted, alternate with the corolla lobes, the anthers 4-loculate, introrse, 2-lobed, the thecae more or less lunate and opposed, the 4 locules equal in length, or 4-lobed, the thecae sulcate, the ventral locules longer than the dorsal and parallel; ovary inferior, basically 3-carpellate, maturing 1 fertile adaxial carpel, the ovule 1, pendulous, anatropous, exalbuminous, the raphe ventral and united, vestigial abaxial carpels 2, the style 1, the stigma 3-lobed, included or exserted. *Fruits* cypselate achenes, adaxial veins 3, 1 median, 2 peripheral, abaxial veins 3, oriented more or less in the median plane.

Valeriana includes about 250 species. Most species occur in the north temperate zone. There is also a concentration of species in South America—principally in the Andean region, with a smaller concentration in southeastern Brazil—and in Europe and the Middle East. The salient taxonomic characters of the genus are in the structure of the inflorescence and the monocarpellate achenes with an epigynous plumose or short-cupuliform calyx limb.

Economic attributes occur in the roots of various taxa. *Valeriana officinalis* L., the type species, has been used for nervousness, suffocation, asphyxiation, migraine, menopause, fevers, and parasites. Among New World taxa, the Mexican species, *V. pratensis* (Benth.) Steud. is known to be used medicinally, and others are probably used locally. The roots when dry emit a characteristic pungent or foetid odor, a trait found in many members of the genus. The odor persists indefinitely in herbarium specimens.

Literature:

Meyer, F. G. 1951. *Valeriana* in North America and the West Indies (Valerianaceae). Ann. Missouri Bot. Gard. 38: 377–503.

a. Stems voluble; inflorescences axillary; stamens included; corolla 0.5–3.0 mm long.
  b. Leaves ternate ..... 3a. *V. scandens* var. *scandens*
  bb. Leaves undivided ..... 3b. *V. scandens* var. *candolleana*
aa. Stems erect or clambering; inflorescences terminal; stamens exserted; corolla 2.3–6.0 mm long; leaves simple or imparipinnate.
  c. Leaves simple; inflorescence diffuse in anthesis; perfect flowers 1.8–5.5 mm long; rhizomatous or with subnapiform roots.
    d. Plants robust, sometimes clambering; leaves longer than wide, elliptic to ovate or suborbicular, acute to acuminate, entire to slightly dentate; inflorescences often widely spreading, pilosulous throughout; rhizomatous ..... 1. *V. clematitis*
    dd. Plants slender, erect; leaves mostly ovate and truncate at the base, serrate to crenate; inflorescences less diffuse with ascending branches, glabrous; taproot subnapiform ..... 4. *V. urticaefolia*
  cc. Leaves imparipinnate; inflorescence subcapitate in anthesis; perfect flowers consistently larger, 4–6 mm long; taproot thickened, often fasciculate, more or less fusiform ..... 2. *V. pulchella*

1. **Valeriana clematitis** H.B.K., Nov. Gen. Sp. Pl. 3: 327. 1819. TYPE: Colombia, *Humboldt & Bonpland* (P).

V. subincisa Benth., Pl. Hartw. 39. 1839. TYPE: *Hartweg 303* (CGE, D, K, NY).
V. pavonii Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 16, *tab. 215*. 1845. TYPE: *Poeppig s.n.* (MO, W).

V. hispida Turcz., Bull. Soc. Imp. Naturalistes Moscou 25: 172. 1852. TYPE: *Jameson 794* (BM, CGE, D, FI, K, MO).
V. pavonii var. *yungasensis* Briq., Annuaire Conserv. Jard. Bot. Genève 17: 337. 1913. TYPE: *Bang 298* (D, MO).
V. ghiesbrechtii Briq., Annuaire Conserv. Jard. Bot. Genève 17: 345. 1914. TYPE: *Ghiesbreght* (D, K, MO, P).
V. laxissima Standley & L. O. Williams, Ceiba 1: 252. 1951. TYPE: *Williams & Allen 16524* (EAP).

Perennial *herbs*, clambering or erect, 3.5–12.0 dm tall from a short rhizome; stems leafy, often profusely branched, rarely unbranched, terete or sometimes quadrangular, becoming suberous or subligneous in age, 2–6 mm thick, scattered-hirtellous, the nodes more densely so, the young lateral branches hoary-puberulent, soon glabrate. *Leaves* cauline, petiolate, undivided, elliptic to ovate or suborbicular, usually somewhat truncate at the base, acute to acuminate or subcaudate, 4–12 cm long, entire or slightly dentate, sparsely to densely pilosulous or subcanescent, especially beneath; blades abruptly expanding, 3.0–10.5 cm long, 1.4–4.8 cm wide; petioles rarely equaling the blades, 1.0–5.6 cm long, sparsely to densely pilosulous or subcanescent. *Inflorescences* aggregate or compound dichasia, more or less pyramidal, the terminal branches 2.6–20.0 cm long, 4.5–16.0 cm wide in anthesis, later diffuse, 8.5–53.0 cm long, 7.5–20 cm wide, the nodes and internodes glabrous or spreading-pilosulous; bracts 1.5–4.0 mm long, reduced above, glabrous or hirtellous. *Flowers* white, gynodioecious; calyx limb 10–12-fid; corolla infundibuliform, in the perfect flowers 2.0–5.5 mm long, in the pistillate flowers 0.9–3.0 mm long, white to pale lavender, glabrous or hirtellous towards the base of the tube without, the lobes half as long as the gibbous tube, the throat sparsely pilosulous within; stamens and style exserted. *Achenes* linear-oblong, somewhat falcate, 2.0–3.5 mm long, 0.9–1.2 mm wide, glabrous, smooth, tawny to rubiginose or purpurascent, abaxial ribs evident.

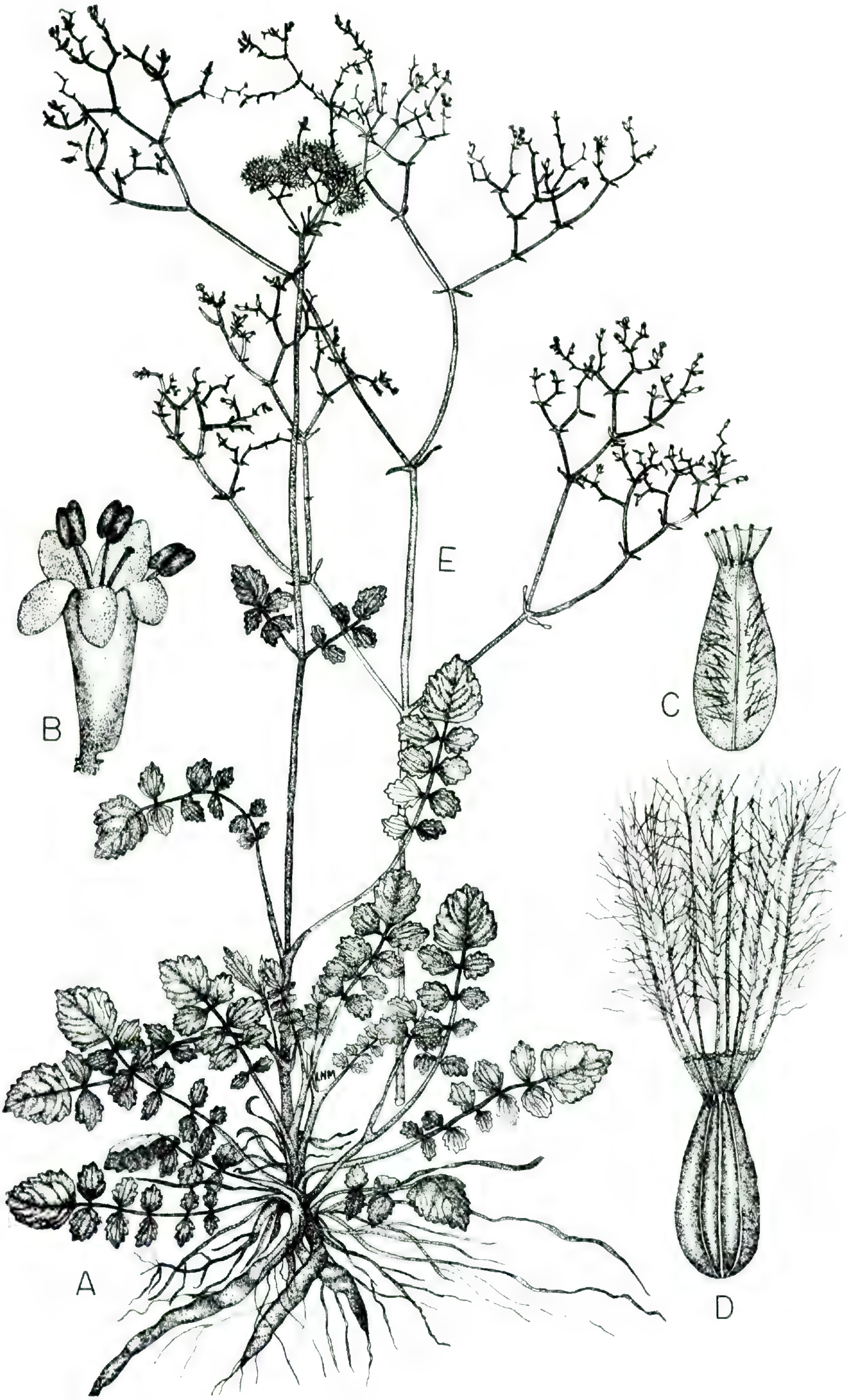
Distributed from northeastern Mexico to Ecuador, *Valeriana clematitis* is a plant of thickets and damp moist woods, often in cloud forests in mountains. Only two collections are known from Panama.

CHIRIQUÍ: Cloud forest between Quebrada Hondo and divide on Caldera-Chiriquicito trail, *Kirkbride & Duke 928* (MO). PANAMÁ: Without definite locality, *Seemann 2133* (BM, K).

2. **Valeriana pulchella** Mart. & Gal., Bull. Acad. Roy. Soc. Bruxelles 11 (1): 123. 1844. TYPE: Mexico, *Galeotti 2560* (BR, G, MO photo).—FIG. 2.

V. woodsonii Standley, Ann. Missouri Bot. Gard. 27: 346. 1940. TYPE: *Woodson, Allen & Seibert 1043* (F, MO, NY).

Perennial *herbs*, 1.5–5.5 dm tall, from simple or forked taproots, often fascicular and more or less fusiform and somewhat verrucose in age, 0.7–1.5 cm thick to 8.5 cm long; caudex covered with marcescent, brownish-papyraceous leaf bases of previous seasons; stems 1–2 mm in diameter, glabrous or sparsely pilosulous, the nodes consistently pilosulous. *Leaves* disposed mostly towards the base, more or less imbricate, sometimes forming a loose rosette, petiolate, pinnate to pinnatifid, oblanceolate to obovate in outline, 6.5–12.2 cm long, 1.5–5.5 cm wide, dentate to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repand or essentially entire, glabrous or glabrescent; terminal lobe abruptly expanded, elliptic to obovate or suborbicular, 1.3–3.4 cm long, 1.4–2.9 cm wide, acute to obtuse, slightly dentate, the lateral lobes 1–5 pairs, 1.0–1.5 cm long, 0.8–1.0 cm wide, dentate, short-petiolulate, often grading smaller towards the base of petiole; petioles 1.5–7.0 cm long. *Inflorescences* compound dichasia, terminal dichotomies 1–2 cm wide in anthesis, later diffuse, ca. 10 cm across in fruit, the nodes usually tufted-pilosulous, the internodes glabrous or scattered-pilosulous; bracts 6–9 mm long, linear-acuminate to spatulate, 2.0–2.5 mm wide. *Flowers* hermaphrodite, pale pink, rarely gynodioecious; calyx limb 11–12-fid or obsolete; corolla infundibuliform, in the perfect flowers 4–6 mm long, in the pistillate flowers 2.5–3.0 mm long, glabrous without, the lobes half as long as the gibbous tube, the throat scattered-pilosulous within; stamens and style exserted. *Achenes* oblong to broadly ovate, sometimes more or less abaxially keeled, 3.0–3.6 mm long, 1.2–2.2 mm wide, smooth, sometimes purplish maculate, glabrous or hirtellous, abaxial ribs prominent.

Fairly uniform throughout its distribution from the mountains of southern Mexico through Guatemala to Panama, this species is most closely related to *V. deltoides* F. G. Meyer of Mexico.

CHIRIQUÍ: Volcán de Chiriquí, Potrero Muleto, *Davidson 1023* (F, GH, MO). W side of Volcán Barú, along trail from lava flats to summit, ca. 3000 m, *Mori & Bolten 7345* (MO). Volcán Barú, Potrero Muleto, ca. 3000 m, *Mori & Bolten 7421* (MO, NA). Vic. of Finca Lérida, *Woodson & Schery 377* (GH, MO). Loma Larga to summit, Volcán de Chiriquí, *Woodson et al. 1043* (F, MO, NY).

3. **Valeriana scandens** L., Sp. Pl., ed. 2. 47. 1762. TYPE: Habitat in Cumaná, Jan. 1755, *Loefling* (not seen).

Perennial *herbs*, voluble or clambering; stems leafy, the lowermost becoming more or less suberous in age, much branched above, 1–3 mm in diameter, the internodes 6–26 cm long, glabrous or sparsely spreading-pilosulous. *Leaves* cauline, petiolate, undivided or ternate, ovate-cordate, apically short- or long-acuminate to acute, sometimes mucronate, 4.5–18.0 cm long, serrate to dentate, repand to entire, glabrous or scattered-pilosulous above, glabrous beneath; blades of the undivided leaves 3.2–11.0 cm long, 2.0–8.8 cm wide, the terminal lobe of the divided leaves ovate to ovate-oblong, 2.2–11.0 cm long, 0.9–6.3 cm wide, the lateral lobes smaller, often somewhat oblique; petioles 1.3–10.2 cm long. *Inflorescences* aggregate dichasia, 12–40 cm long, glabrous or sometimes densely pilosulous; bracts 1.7–2.5 cm long, glabrous or sometimes densely pilosulous. *Flowers* white, gynodioecious; calyx limb 11–15-fid; corolla more or less campanulate-infundibuliform, the perfect flowers 1.0–2.3 mm long, the pistillate flowers 0.5–1.0 mm long, glabrous without, the lobes less than half the length of the gibbous tube, the throat

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FIGURE 2. *Valeriana pulchella* Mart. & Gal.—A. Habit (×⅖).—B. Flower (×8⅖). [After *Woodson & Schery 377* (MO).]—C. Mature achene, adaxial side (plumose calyx deleted) (×8⅖).—D. Mature achene, abaxial side (×8⅖).—E. Fruiting branch (×⅖). [After *Breedlove 6850* (NA), Mexico.]

scattered-pilosulous or glabrous within; stamens and style exserted. *Achenes* oblong-linear to oval, subfabriliform (bellows shape), with 2 relatively prominent subperipheral and 1 median abaxial vein, 1.9–3.1 mm long, 1–2 mm wide, smooth, tawny to brownish, sparsely pilosulous on the adaxial side, glabrous on the abaxial side.

Valeriana scandens ranges widely from southern Florida to the Greater Antilles, from Mexico to Panama, and in South America from Venezuela throughout the Andean region, except Chile, to southern Brazil and northern Argentina. In Panama, as in other areas, *V. scandens* may be separated into two distinct leaf variants, i.e., plants with simple leaves and those with ternate leaves, although these variants are usually sympatric. Of the two, the ternate-leaved variant appears to be more common in most areas.

3a. **Valeriana scandens** var. **scandens.**

V. volubilis Ses. & Moc. ex DC., Prodr. 4: 634. 1830, nom. nud.
V. phaseoli Braun, Ind. Sem. Hort. Berol. 13 (App. 2). 1851. TYPE: *Chrismar* (not seen).
V. scandens α genuina Muell. in Mart., Fl. Bras. 6 (4): 344. 1855.
V. scandens β angustiloba Muell. in Mart., Fl. Bras. 6 (4): 344. 1885. TYPE: *Mueller 769* (NY, W).
V. scandens δ dentata Muell. in Mart., Fl. Bras. 6 (4): 344, pro parte. TYPE: not seen.

Perennial *herbs*, voluble or clambering; stems leafy, much branched above. *Leaves* ternate; terminal lobe ovate to ovate-oblong, 2.2–11.0 cm long, 0.9–6.3 cm wide, the lateral lobes smaller, often somewhat oblique; petioles 1.3–10.2 cm long.

The typical and more common variety, with ternate leaves, appears to be rare in Panama, although it is common elsewhere in Central America.

BOCAS DEL TORO: Río Teribe between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 466* (MO).

3b. **Valeriana scandens** var. **candolleana** (Gard.) Muell., Fl. Bras. 6 (4): 344. 1885.

V. alpina Vell., Fl. Flum. 28. 1825; Atlas 1: *tab. 68*. 1827. TYPE: not seen.
V. candolleana Gard., London J. Bot. 4: 112. 1845. TYPE: *Gardner 461* (BM, K, W, MO photo).
V. mikaniae Lindl., J. Hort. Soc. London 3: 316. 1848. TYPE: *Skinner s.n.* (CGE, MO photo).
V. scandens δ dentata Muell. in Mart., Fl. Bras. 6 (4): 344, pro parte. TYPE: not seen.

Perennial *herbs*, voluble or clambering; stems leafy, much branched. *Leaves* undivided, ovate-cordate, short- or long-acuminate, acute, sometimes mucronate, 4.5–18.0 cm long, serrate to crenate, dentate to repand or essentially entire, glabrous or scattered-pilosulous above, glabrous beneath; blades 3.2–11.0 cm long, 2.0–8.8 cm wide.

In Panama, var. *candolleana* appears to be the more common variant.

CANAL ZONE: Near river on island, *White 153* (MO). CHIRIQUÍ: Vic. of "New Switzerland," central valley of Río Chiriquí Viejo, *Allen 1419* (GH, MO, NY). Hill N of Audubon Cabin, *Croat 13662* (MO). From Paso Canoas to Cañas Gordas, 9 mi from Paso Canoas, *Croat 22208* (MO). Methodist Youth Camp between Nueva Swissa and Cerro Punta, *Croat 26266*

(MO). Baja Chorro, Boquete, *Davidson 443* (F, GH, MO). Volcán de Chiriquí, Boquete District, *Davidson 886* (F, GH). From Boquete to 3 mi N, 3300–4200 ft, *Lewis et al. 317* (MO, US). Los Siquas, *Pittier 3188* (F). Río Ladrillo above Boquete, *Pittier 3288* (US). Boquete District, Salla-Camiseta, *Terry 1367* (F, GH, MO). Halfway between Cerro Punta and Bambito, 5600 ft, *Wilbur et al. 10928* (MO, US). Finca Lérida, *Woodson & Schery 225* (GH, MO). Vic. of Callejón Seco, Volcán de Chiriquí, *Woodson & Schery 488* (GH, MO). Bajo Mona, mouth of Quebrada Chiquero, along Río Caldera, *Woodson et al. 999* (MO, NY). COCLÉ: Foothills of Cerro Pilón, near El Valle, 900 m, *Duke & Correa 14708* (MO). El Valle, *Dwyer 1921* (MO). Above El Valle, *Ebinger 1127* (MO). El Valle de Antón, 1000–2000 ft, *Lewis et al. 2521* (MO). DARIÉN: Caná, *Williams 726* (NY).

4. **Valeriana urticaefolia** H.B.K., Nov. Gen. Sp. Pl. 3: 330. 1819. TYPE: Colombia, *Humboldt & Bonpland 2093* (MO, P).

V. scorpioides DC., Prodr. 4: 635. 1830. TYPE: *Berlandier 1133* (BM, D, G, MO).
V. erysimoides Poepp. & Endl., Nov. Gen. Sp. Pl. 3: 16. 1844. TYPE: *Poeppig 1670* (MO photo, W).
V. rhomboidea E. L. Greene, Pittonia. 1: 154. 1888. TYPE: *Forrer s.n.* (F, GH, NA, NY, UC, US).
V. sallei Briq., Annuaire Conserv. Jard. Bot. Genève 17: 339. 1914. TYPE: *Sallé 71* (G).

Annual *herbs*, 1.3–7.5 dm tall, slender, from a subnapiform, 3–8 mm thick, taproot; stem moderately leafy, unbranched or sometimes branched, 0.5–4.0 mm thick, minutely puberulent to densely spreading-pilosulous towards the base, glabrescent above. *Leaves* cauline, 3–7 pairs, sessile or short-petiolate, undivided, ovate to oblong-elliptic to suborbicular, sometimes more or less flabelliform, acute to obtuse, 0.9–9.2 cm long, serrate to crenate, dentate to repand or essentially entire, uniformly spreading-pilosulous, especially above, sometimes more or less restricted to the veins beneath; blades more or less abruptly expanded, 0.7–5.0 cm long, 0.7–4.5 cm wide; petioles 0.2–6.0 cm long or obsolete, rarely exceeding the blades in length, uniformly spreading-pilosulous. *Inflorescences* aggregate or sometimes compound dichasia, more or less flat topped, 2–28 cm long in anthesis, later diffuse, 13–60 cm long, 7–28 cm wide, the terminal scorpioid sympodia 2–6 cm long; bracts 1–2 mm long, glabrous. *Flowers* white to pinkish, hermaphroditic; calyx limb 10–13-fid; corolla infundibuliform to subsalverform, 1.8–5.0 mm long, glabrous without, the tube abruptly narrowed and often somewhat filiform towards the base, the lobes less than half the length of the gibbous tube, the throat sparsely pilosulous without; stamens and style exserted. *Achenes* oval to suborbicular, somewhat fabriliform (bellows shape), with 2 peripheral and 1 median abaxial vein, subarcuate, minutely papillate, yellowish to purplish maculate, 1.2–2.0 mm long, 0.9–1.1 mm wide, glabrous or sometimes densely hirtellous on the adaxial side, glabrous on the abaxial side, the midribs prominent.

Distributed from northern Mexico to Panama, this species also occurs in South America in the Andes from Colombia to Peru. It is rare in Panama.

CHIRIQUÍ: Large old lava flow, ca. 3 km NE of El Hato del Volcán, 1500–1800 m, *Davidse & D'Arcy 10380* (MO, NA). Lava fields near the town of Volcán, ca. 4600 ft, *Duke 9173* (MO). Bajo Mona, Boquete District, 5400 ft, *Terry 1300* (MO).

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FLORA OF PANAMA[1]

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part IX

FAMILY 183. CAMPANULACEAE[2]

ROBERT L. WILBUR[3]

Annual or perennial *herbs*, *shrubs*, or rarely small *trees* with either watery or more typically milky sap. *Leaves* simple, exstipulate, mostly alternate, sessile or more typically petiolate. *Inflorescences* fundamentally determinate, dichasial or monochasial cymes but appearing racemose or thyrsiform or the flowers often solitary in the axils of leaves or bracts and usually pedicellate, often bibracteolate, rarely sessile in compact spikes or heads. *Flowers* usually bisexual, actinomorphic to strikingly zygomorphic; calyx gamosepalous, the lobes (3)5(10), imbricate or valvate; corolla usually gamopetalous, rarely lacking or polypetalous, (3)5(6)-parted, valvate (imbricate in the anomalous genus *Sphenoclea*), campanulate or tubular to conspicuously bilabiate; stamens (3)5(6) with the filaments rarely distinct or more typically connate as in all Panamanian genera except *Sphenoclea*, epipetalous basally or completely free from the corolla and alternating with its lobes, the anthers dehiscing longitudinally and introrsely, distinct or connate, biloculate; pistil 1 with 2(3) or 5 carpels, the style 1 and stigmas or stigmatic lobes usually 2(5); ovary inferior, rarely superior, 1–10-loculate but mostly with 2(5) locules and axile placentation except in unilocular genera with parietal placentae. *Fruits* capsules, commonly dehiscing either by apical slits or lateral pores or rarely circumscissilely, occasionally berries; seeds small, anatropous, numerous and usually with a straight embryo and abundant, fleshy endosperm.

This is a widely distributed family of approximately 60 genera and perhaps 2,000 species most abundantly represented in the montane tropics and subtropics. The Campanulaceae is sometimes divided into several families with the Lobeliaceae and Sphenocleaceae most frequently segregated. The more inclusive and conservative circumscription of the family is adopted in this treatment.

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[1] Assisted by National Science Foundation Grant BMS 72-02441 A03 (Thomas B. Croat, principal investigator).

[2] Grateful acknowledgment is made to the Duke University Research Council and especially to the National Science Foundation (GB-13815) for their assistance which made this study feasible. My heartfelt thanks should also be expressed to the curators of the herbaria listed below whose willingness to lend specimens, often for an extended period, made this study possible: A, C, CR, DUKE, F, FSU, GH, LL, M, MICH, MO, NY, PMA, REED, SCZ, WIS.

[3] Department of Botany, Duke University, Durham, North Carolina 27706.

ANN. MISSOURI BOT. GARD. 63: 593–655. 1976.

REED, cited occasionally as repository for plant specimens, indicates the private herbarium of Clyde F. Reed, 10105 Harford Road, Baltimore, Maryland, U.S.A.

Literature:

McVaugh, Rogers. 1943. Campanulales: Campanulaceae-Lobelioideae. N. Amer. Fl. 32A: 1–134.

Schönland, S. 1889. Campanulaceae. *In* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien IV, 5: 40–70.

Wimmer, F. E. 1943. Campanulaceae-Lobelioideae. *In* Das Pflanzenreich IV. 276b (Heft 106): 1–260.

———. 1953. Campanulaceae-Lobelioideae. *In* Das Pflanzenreich. Heft 107: 261–813.

———. 1968. Campanulaceae-Lobelioideae. Supplementum. *In* Das Pflanzenreich. Heft 108: 814–916.

KEY TO THE GENERA

a. Anthers distinct (i.e., not laterally cohering to one another); filaments distinct; flowers sessile, borne in a compact spike, the flowers contiguous ---------- 7. *Sphenoclea*

aa. Anthers laterally united; filaments monodelphous at least distally; flowers pedicellate, not borne in a dense spike, the flowers not contiguous.

b. Fruit a capsule dehiscing by apical valves.

c. Corolla tube not deeply cleft dorsally, the depth of the dorsal sinus about equalling that of the lateral ones.

d. Ovary partially or wholly inferior with at least the lower half adherent to the hypanthium; corolla somewhat persistent but neither hyaline nor distended by the capsule; annual or perennial herbs or shrubs.

e. Corolla white, salverform, the lobes subequal, the tube 5 cm long or longer ---------- 4. *Hippobroma*

ee. Corolla normally blue, red, yellow, or greenish but not white, never salverform, the lobes strikingly dissimilar in size and shape and the tube less than 3.5 cm long.

f. Corolla blue or purplish blue; pedicels 2 cm long or less; seeds smooth and shining ---------- 5. *Lobelia*

ff. Corolla purplish to reddish or orange but never bluish; pedicels 4 cm long or longer in fruit; seeds minutely foveate-reticulate ---------- 6. *Siphocampylus*

dd. Ovary superior or nearly so, the hypanthium very short and only attached to the ovary at the base; corolla becoming hyaline and much distended by the enlarging capsule; slender annual herbs ---------- 3. *Diastatea*

cc. Corolla tube cleft at least halfway to the base on the dorsal side, the sinus thus formed much deeper than the lateral sinuses ---------- 5. *Lobelia*

bb. Fruit a dry or fleshy berry, indehiscent.

g. Anther tube not constricted at the orifice but obliquely open, the anthers naked or sparsely densely soft-pilose at the tips but never with tufts of stiff bristly trichomes; style jointed above the ovary and deciduous together with the corolla and stamens from the developing fruit; pedicels ebracteolate; seeds oblong to fusiform, much longer than wide, with a surface network of slightly elongate depressions parallel with long axis of seed ---------- 1. *Burmeistera*

gg. Anther tube somewhat rounded at the apex, the orifice partially closed and usually appearing lateral due to the inturned tips of the longer anthers, the two shorter anthers densely bristly tufted or with a triangular appendage at the tip; style usually persisting together with the withering corolla and stamens on the

developing fruits; pedicels usually bibracteolate; seeds lenticular, little longer than wide, with a surface network of nearly flat-bottomed and isodiametric depressions ..... 2. *Centropogon*

ARTIFICIAL KEY TO THE GENERA—With emphasis on floral features

a. Leaves entire; anthers and filaments distinct (i.e., neither the filaments nor the anthers laterally coherent); flowers sessile and borne in a compact and congested spike ..... 7. *Sphenoclea*

aa. Leaves coarsely toothed, serrulate or denticulate; anthers and filaments coherent (i.e., the filaments monadelphous at least distally and the anthers laterally fused); flowers pedicellate, not borne in a dense spike of congested, contiguous flowers.

b. Pedicels ebracteolate.

c. Annual erect herbs less than 5(–8) dm tall; corollas blue to whitish; flowers less than 1 cm long; anther tubes less than 2 mm long; ovary ¾ or more superior; seeds shiny ..... 3. *Diastatea*

cc. Perennial herbs usually more than 5 dm tall, if erect, or stems sprawling or ascendent; corollas yellow, reddish or greenish but never bluish; anther tubes usually more than 2 mm long; ovary ¾ or more inferior; seeds reticulate.

d. Corollas greenish or greenish tinged with dark purple or russet red but never bright red; anther tube not constricted at the orifice but obliquely open, the anthers naked or sparsely to densely soft-pilose apically, never with tufts or stiff bristly trichomes; style jointed above the ovary and deciduous together with the corolla and stamens from the developing fruit; seeds oblong to fusiform with a surface network of slightly elongate depressions parallel to the long axis of the seed ..... 1. *Burmeistera*

dd. Corolla bright red to scarlet, sometimes drying reddish purple; anther tube somewhat rounded apically, the orifice partially closed and appearing lateral due to the inturned tips of the longer anthers, the two shorter anthers with a tuft of stiff bristles; styles usually persisting together with the withered corolla and stamens on the developing fruit; seeds lenticular, little longer than wide with a surface network of isodiametric depressions.

e. Fruits indehiscent, dry or fleshy berries ..... 2. *Centropogon*

ee. Fruit capsules with apical dehiscence ..... 6. *Siphocampylus*

bb. Pedicels bracteolate.

f. Corolla white, salverform; the corolla lobes subequal, the tube 5 cm or more long; filaments attached to the corolla tube at a point well above the upper quarter ..... 4. *Hippobroma*

ff. Corolla blue, red, yellow, greenish or purplish but not white, never salverform; the corolla lobes strikingly dissimilar in size and shape, the tube less than 5 cm long; filaments attached to the corolla tube in its lower third or free from it.

g. Corolla tube cleft at least halfway to the base on the dorsal side and the sinus thus formed much deeper than the lateral sinuses; filaments free from the corolla ..... 5. *Lobelia*

gg. Corolla tube not cleft on the dorsal side to beyond the middle of the tube; filaments attached to the base of the corolla tube.

h. Fruit an indehiscent or fleshy berry ..... 2. *Centropogon*

hh. Fruit a capsule with apical dehiscence ..... 6. *Siphocampylus*

1. BURMEISTERA

Burmeistera Triana, Nuevos Jeneros Espec. 13. 1854. TYPE: *B. ibaguensis* Triana.

Epiphytic or terrestrial, suffrutescent *herbs* or soft woody *shrubs*. *Leaves* simple, exstipulate, alternate, petiolate, pinnately veined and usually denticulate or serrulate. *Flowers* solitary in the axils of the upper leaves on ebracteolate pedicels or more rarely corymbose; corolla green, yellow, purplish to reddish brown, the

tube neither dorsally cleft nor fenestrate, expanded basally and near throat but with a somewhat constricted waist, the lobes falcate, all bent away from the dorsal side of the flower with the two dorsal lobes the longest and the ventral lobe usually the shortest; filament basally distinct, either basally adherent or free from the corolla, the anther tube with an enlarged, oblique, terminal orifice, the anthers either all terminally naked or some or all of the anthers with a few pilose trichomes or the two lowermost with a dense tangle of villous trichomes but never with a terminal tuft of stiff bristles or a cartilaginous triangular scale; style jointed just above ovary and deciduous with the corolla and stamens, the ovary apically truncate or nearly so. *Fruits* berrylike, occasionally much inflated at maturity; seeds numerous, oblong or ovoid to fusiform, 0.7–1.3 mm long, much longer than wide, minutely foveate-reticulate and the reticulations elongate parallel to the long axis of the seed.

This is a taxonomically difficult American genus of about 80 species ranging from Guatemala south throughout Andean South America to Peru.

It is the largest genus of Campanulaceae in the Panamanian flora. A large number of species have recently been collected in isolated mountain ranges of the Darién. Another inadequately sampled area of surprising diversity is along the divide between Bocas del Toro and Chiriquí. Scientists would be well advised to collect carefully and consistently specimens of this little-collected and poorly understood genus.

Literature:

Wilbur, Robert L. 1975. A synopsis of the Costa Rican species of *Burmeistera* (Campanulaceae: Lobelioideae). Bull. Torrey Bot. Club 102: 225–231. [1976].

a. Median cauline leaves more than 8 times as long as wide, narrowly linear ..... 1. *B. chiriquiensis*

aa. Median cauline leaves less than 6 times as long as wide.

b. Anthers pilose externally with golden trichomes; plants vegetatively entirely glabrous ..... 8. *B. microphylla*

bb. Anthers either glabrous externally or with white or sordid, grayish trichomes; plants vegetatively either glabrous or pubescent.

c. Flowers less than 3 cm long.

d. Filament tube 10 mm long or more; hypanthium 3–6 mm long; corolla yellow or greenish.

e. Corolla yellow; calyx lobes acute, deltoid; filament tube inconspicuously puberulous distally ..... 11. *B. parviflora*

ee. Corolla greenish; calyx lobes obtuse, oblong; filament tube glabrous distally ..... 9. *B. morii*

dd. Filament tube less than 9 mm long; hypanthium ca. 3 mm long; corolla purplish ..... 7. *B. kirkbridei*

cc. Flowers 3 cm or longer.

f. Hypanthium in anthesis cylindric to campanulate or urceolate, somewhat rounded at the base and with the sides more or less parallel.

g. Leaves lanceolate to lance-ovate, gradually long-acuminate from below the middle, 2.5 cm wide or less; plants vegetatively glabrous .. 6. *B. glauca*

gg. Leaves elliptic, ovate or broadly lanceolate, usually wider than 2.5 cm; plants vegetatively usually somewhat puberulent or scaberulent.

h. Calyx lobes 5 mm long or less.

i. Corolla puberulous; calyx lobes and hypanthium spiculate to puberulous; berry red ..... 5. *B. dukei*
ii. Corolla glabrous; calyx lobes and hypanthium glabrous; berry white or greenish turning blackish.
j. Upper corolla lobes less than 12 mm long and the 2 lateral lobes about 7 mm long; corolla greenish; anthers externally puberulous ..... 12. *B. pirrensis*
jj. Upper corolla lobes 18 mm long or longer and the 2 lateral lobes 12–14 mm long; corolla dark red; anthers externally glabrous ..... 3. *B. darienensis*

hh. Calyx lobes usually more than 5 mm long.
k. Two lower anthers densely bearded apically with a dense tangle of trichomes; leaves mostly 5 cm or more wide; plants of Darién ..... 10. *B. panamensis*
kk. Two lower anthers sparingly fringed apically or glabrous with not more than a sparse fringe of trichomes; leaves mostly less than 5 cm wide; plants from west of Darién.
l. Corolla green or bronzy; hypanthium and calyx lobes green, drying green or stramineous, rarely suffused with purple or maroon; berry greatly inflated with a thin, bladdery wall, 2–4 cm in diameter and 2.5–5 cm long ..... 16. *B. vulgaris*
ll. Corolla predominately purplish or green with a deep suffusion of maroon or dark purple; hypanthium and calyx lobes purplish and drying dark purplish or blackish; berry fleshy and with a substantial, thick wall, 1–2(–2.5) cm in diameter and 1–2(–3) cm long ..... 2. *B. cyclostigmata*

ff. Hypanthium in anthesis obconic, acutely tapering at the base with the sides strongly divergent.
m. Corolla tube puberulent or inconspicuously appressed short-pubescent.
n. Pedicels and hypanthia glabrous to moderately spiculate or appressed short-pubescent or even strigillose; Panama east of Volcán Chiriquí ..... 4. *B. dendrophila*
nn. Pedicels and hypanthia moderately to densely spreading short-pubescent; Panama west of Volcán Chiriquí ..... 15. *B. utleyi*

mm. Corolla tube glabrous.
o. Calyx lobes narrowly linear, (7–)11–20 mm long and about 1–1.5 (–2) mm wide, equalling or longer than the hypanthium ..... 13. *B. tenuiflora*
oo. Calyx lobes triangular-dentate to lanceolate, ovate or oblong, if linear then 10 mm long or less and often wider than 1–2 mm.
p. Filaments distally glabrous; anther tube externally glabrous; upper corolla lobes 7 mm long ..... 14. *B. toroensis*
pp. Filaments distally puberulous; anther tube externally puberulous; upper corolla lobes 10 mm long or longer ..... 4. *B. dendrophila*

1. **Burmeistera chiriquiensis** Wilbur.[4] TYPE: Panama, *Kirkbride & Duke 956* (MO, holotype).

Epiphytic suffrutescent *herbs* or *shrublets*; stems glabrous. Principal *leaves* with blades narrowly linear, 10–12.5 cm long, 7–10 mm wide, ca. 10–15 times as

[4] *Burmeistera chiriquiensis* Wilbur, sp. nov. Planta glaberrima, epiphytica. Lamina foliorum lineare, glabra, circa 10–12.5 cm longa et 7–10 mm lata, ca. 10–15-plo longiora quam lata, acuminata ad apicem et basi cuneata; petioli glabri, 0.5–1.0 cm longi. Flores solitarii, 3–3.5 cm longi; pedicelli glabri, ca. 3 cm longi. Hypanthium obconicum, glabrum; lobi calycis lineari, 7–9 mm longi et 0.5–0.8 mm lati. Corolla glabra, atroviolacea vel virenta. Filamenta ca. 23 mm longa; anthearum tubus 2–4.5 mm longus, 2 antherae inferiores in apice villosa-barbatae.

long as wide, apically acuminate and tapering into an elongate, caudate tip 2–3 cm long, basally gradually tapering, marginally shallowly dentate with 1–2 inconspicuous teeth per cm, glabrous on both surfaces; petioles slender, glabrous, 0.5–1 cm long. *Flowers* solitary in the upper leaf axils, 3–3.5 cm long; pedicels spreading to ascendant, glabrous, ebracteolate, ca. 3 cm long; hypanthium in anthesis obconic, 5–6 mm long, 3 mm at its broadest diameter, glabrous; calyx lobes narrowly linear, 7–9 mm long, 0.5–0.8 mm wide, acute, inconspicuously callous-denticulate; corolla glabrous, greenish to dark purplish, the tube ca. 14 mm long, basally ca. 4 mm in diameter and tapering above to ca. 2 mm in diameter, the throat flaring ca. 7 mm in diameter, the lobes broadly oblong-falcate with the 2 upper lobes 11–13 mm long, the 2 lateral lobes ca. 7 mm long, the lowermost lobe ca. 5 mm long; filament tube ca. 23 mm long, glabrous throughout or very sparsely and inconspicuously puberulent distally, the longer anthers ca. 4.5 mm long, the shorter anthers ca. 2 mm long, all glabrate except for puberulence in the sutural grooves and the dense tangle of pilose trichomes on the upper edge of the lower anthers. *Berries* and seeds unknown.

This species is known only from the holotype collected on the border between Bocas del Toro and Chiriquí. The linear leaves are unlike those of any other species of Central American *Burmeistera*.

CHIRIQUÍ: Cloud forest between Quebrado Hondo and divide on Chiriquicito-Caldera Trail, *Kirkbride & Duke 956* (MO).

2. **Burmeistera cyclostigmata** Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 291. 1895. TYPE: Costa Rica, Prov. de Cartago, Estrella, *Cooper 5845* (US, holotype; GH, isotype).

B. cyclostigmata var. *suerrensis* Donnell Smith, Bot. Gaz. (Crawfordsville) 24: 394. 1897. TYPE: Costa Rica, Prov. de Limón, llanos de Santa Clara, *Donnell Smith 6623* (US, holotype; GH, M, isotypes).
B. suerrensis (Donnell Smith) F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 14. 1932.
B. suerrensis var. *almirantensis* F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 14, *pl. 124, fig. 26.* 1932. TYPE: Panama, *Cooper 234* (F, holotype; NY, US, isotypes).
B. millei F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 15, *pl. 123, fig. 12.* 1932. SYNTYPES: Ecuador, locality not indicated, *Mille 31, 32* (Q, not seen).

Terrestrial or epiphytic, suffrutescent *herbs*; stems usually (0.3–)1.0–1.5 m high, glabrous throughout or minutely pubescent above. Principal *leaves* with blades elliptic, ovate or broadly lanceolate, (2–)7–12(–18) cm long, (1.2–)3.5(–8) cm wide, usually 2–3 times as long as wide, apically abruptly narrowed to an acuminate tip, basally cuneate to rounded, marginally entire except for minute callosities or repand-dentate with conspicuous callose-tipped teeth, glabrous on both surfaces, the veins minutely scaberulous beneath, rarely puberulous to short-pubescent beneath; petioles glabrous, rarely puberulous, (1–)1.5–3 cm long. *Flowers* (3–)4–5 cm long; pedicels solitary in the upper leaf axils, ascending, glabrous, ebracteolate (1.5–)4.5–10(–12) cm long; hypanthium glabrous, rarely appressed puberulous or spiculate, in anthesis cylindric to campanulate, basally rounded, flaring apically, usually as broad as long, 5–12 mm long, 4–8 mm

in diameter; calyx lobes oblong, linear or rarely triangular-deltoid, apically rounded, rarely acute, entire or minutely dentate, 2–12(–22) mm long; corolla glabrous, rarely puberulous or spiculate, variable in color but basically green with suffusion of red or dark purple, appearing deep maroon or dark purple, the tube 11–16 mm long, flaring greatly in the upper third, the lobes linear and falcate, the 2 upper lobes 12–22 mm long, the 2 lateral lobes 8–12 mm long, the lowest lobe 6–9 mm long; filament tube (25–)30–36 mm long, glabrous or distally inconspicuously puberulous, basally distinct and free from the corolla tube, the anthers usually glabrous externally, rarely copiously appressed-pubescent, the 3 longer anthers 5–8 mm long, the 2 shorter anthers about half as long and either glabrous or sparsely pilose apically. *Berries* fleshy or watery, white and often tinged with purple or blue, ovoid with truncate ends to broadly ellipsoid, 10–15 (–30) mm long, 6–20(–25) mm in diameter; seeds ellipsoid-oblong with rounded ends, 0.6–1.0 mm long, light brown.

This species is known from Costa Rica south to central Panama and from Colombia and Ecuador. Its great variability in size and shape of the calyx lobes has been emphasized by taxonomists in recognizing the variants listed in the above synonymy. Those forms with rounded calyx lobes 5 mm long or less have been referred to as either *Burmeisteria cyclostigmata* var. *suerrensis* or *B. suerrensis* while *B. suerrensis* var. *almirantensis* was characterized by similarly short but acute calyx lobes. Forms with longer calyx lobes were treated as *B. cyclostigmata.* There is no geographic segregation between plants with short and long calyx lobes, and the range in calyx-lobe lengths seems to represent a morphological continuum. A specimen from La Peña de Zarcero, Prov. de Alajuela, Costa Rica (*Austin Smith 893* (NY)) was assigned by Wimmer (1968) to *Burmeistera mindoana* F. E. Wimmer, although in his opinion it was different somewhat from the specimens known from Ecuador and Colombia. This specimen falls well within the range of variation exhibited by *B. cyclostigmata.*

BOCAS DEL TORO: Region of Almirante, *Cooper 234* (F, NY, US). Chiriquí Trail between Quebrado Menaco and Buena Vista, *Kirkbride & Duke 674* (REED). Fish Creek Mts., vic. of Chiriquí Lagoon, *von Wedel 2285* (GH, MO, US). CHIRIQUÍ: Cerro Pando at the Costa Rican-Panamanian border, 2000–2482 m, *Mori & Bolten 7323* (DUKE, MO). Cerro Hornitos, ca. 15 km NE of Gualaca, ca. 2200 m, *Mori & Bolten 7483* (MO). Valley of the upper Río Chiriquí Viejo, *White 20* (MO). COCLÉ: Cerro Pilón, *Croat 14347* (DUKE, MO). N slope and summit of Cerro Pilón, 900–1173 m, *Croat 22928* (DUKE, MO). Cerro Caracoral, *Duke & Dwyer 15140* (REED). Cerro Pilón, 3000 ft, *Duke & Lallathin 15026* (MO). Cerro Pilón below summit, 2000–2700 ft, *Dwyer et al. 4524* (DUKE, MO). Cerro Pilón, *Kirkbride 1056* (MO). Cerro Caracoral, *Kirkbride 1115* (MO). Cerro Pilón, *Lallathin 5082* (MO). Cerro Pilón, 5 km NE of El Valle, *Mori 6623, 6624* (both DUKE, MO). VERAGUAS: Cerro Tute, vic. of Santa Fé, 3000 ft, *Allen 4346* (MO). 5 mi NW of Santa Fé, 700–1200 m, *Croat 23178* (DUKE). Santa Fé subiendo hacia Cerro Tute, *Mendieta 557* (DUKE), *576, 577* (both PMA). Slopes of Cerro Tute, NW of Santa Fé, 1 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 4795* (DUKE, MO). NW of Santa Fé, below Cerro Tute peak, *Mori & Kallunki 5244* (MO). Below summit of Cerro Tute, *Mori & Kallunki 5271* (DUKE, MO). 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3221* (DUKE, MO). Stream NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3917* (DUKE, MO). Cerro Tute, ca. 5 km NW of Santa Fé, 1100–1400 m, *Mori et al. 7584* (MO), 7585 (DUKE, MO). Cerro Tute, above 1000 m, *Mori 6746* (DUKE, MO). 16 km from Santa Fé toward Calovebora, *Mori 6680* (DUKE, MO). Trail up E side of Cerro Tute, to 1200 m, *Witherspoon 8862* (MO).

3. **Burmeistera darienensis** Wilbur.[5] TYPE: Panama, *Gentry 4600* (MO, holotype).

Suffruticose epiphytic *shrublet*; branchlets glabrous. Principal *leaves* with blades narrowly elliptic to lanceolate, (9–)12–17 cm long, 3–5 cm wide, ca. 3–4 times as long as wide, apically acute, basally cuneate to somewhat rounded, marginally indistinctly callose-serrulate with 1–2 shallow teeth per cm, glabrous above and sparingly to moderately microscopically puberulous on the principal veins beneath, appearing completely glabrous without good lighting and magnification; petioles 1.0–2.2 cm long, glabrous. *Flowers* ca. 4 cm long; pedicels solitary in the upper leaf axils, erect to ascendant, slender, glabrous, ebracteolate, 3–5 cm long; hypanthium in anthesis cylindric, glabrous, ca. 7 mm long, 4 mm in diameter; calyx lobes ovate to oblong, obtuse, entire, glabrous, 2–3 mm long, ca. 2 mm wide; corolla glabrous, dark red, the tube 10–12 mm long, 3 mm in diameter, the lobes linear-oblong, the 2 upper lobes 20–22 mm long, the 2 lateral lobes 12–14 mm long, the lowermost lobe ca. 10 mm long; filament tube distally slightly pilosulose, ca. 2.5 cm long, the anther tube externally glabrous, the 2 lower anthers with a thin pilose fringe. *Berries* globose, ca. 1.5 cm in diameter.

This species is known only from Darién Province.

DARIÉN: Cloud forest and/or mossy forest, 2500–4500 ft, *Duke & Elias 13835* (MO, in part). Summit of Cerro Pirre, ca. 1000 m, *Gentry 4600* (MO). Summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7106* (DUKE).

4. **Burmeistera dendrophila** F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 23, *pl. 124, fig. 18.* 1932. TYPE: Panama, *Pittier 3253* (US, holotype).

Epiphytic to terrestrial, suffrutescent *herbs*; stems 30–50 cm high, minutely puberulent throughout excepting the lower stem. Principal *leaves* with blades elliptic, 4–10(–14) cm long, mostly 2.5–4 times as long as wide, usually apically acuminate or acute but rarely blunt, basally cuneate-tapering, marginally repand-denticulate with ca. 3 inconspicuous callosities per cm, glabrous to inconspicuously and minutely puberulent above and on the veins beneath; petioles 1–3 cm long, appressed puberulent. *Flowers* 4.5–5 cm long; pedicels solitary in the upper leaf axils, ascending, sparingly puberulent to glabrous, ebracteolate, 4–7 cm long; hypanthium at anthesis obconic, glabrous to sparingly and minutely appressed-puberulent, basally acute to slightly rounded and usually with strongly divergent sides, (4–)6–9 mm long, 3–6 mm in diameter; calyx lobes ovate, obtuse, entire to obscurely rounded-denticulate with 2–4 teeth per side, glabrous to sparingly and inconspicuously short-pubescent, 2.5–3.5 mm long; corolla exter-

[5] *Burmeistera darienensis* Wilbur, sp. nov. Planta suffruticosa, epiphytica; ramuli glabri. Lamina foliorum elliptica vel lanceolata, (9–)12–17 cm longa et 3–5 cm lata, ca. 3–4-plo longiora quam lata, acuta apicem et basi cuneata vel rotundata, margine calloso-serrulata 1–2 serrulatis per cm, nervis subtus puberulis; petioli glabri, 1.0–2.2 cm longi. Flores ca. 4 cm longi; pedicelli glabri, 3–5 cm longi. Hypanthium cylindricum, glabrum, ca. 7 mm longum et 4 mm latum; lobi calycis ovati vel oblongi, obtusi, integri, glabri, 2–3 mm longi et ca. 2 mm lati. Corolla glabra, atroviolacea; tubi 10–12 mm longi et 3 mm lati; lobi linearo-oblongi, superiori 20–22 mm longi, laterali 12–14 mm longi et inferiori ca. 10 mm longi. Filamenta pilosulosa, ca. 2.5 cm longa; anthearum tubus glaber. Bacca globosa, ca. 1.5 cm longa et lata.

nally glabrous to appressed puberulent or strigillose, light green to dark purple, the tube 12–18 mm long and 1.5–3 mm in diameter, the lobes falcately oblong to broadly ovate, acute to acuminate, the 2 upper lobes 12–18 mm long, the 3 lower lobes 7–10 mm long; filament tube exserted, 32–40 mm long, mostly glabrous although distally puberulous, the anthers ca. 5 mm long, externally puberulous, the 2 shorter anthers apically with a few white trichomes. *Berries* turbinate, ca. 12 mm high, 10 mm in diameter at apex; seeds dark brown, flattened, pitted, 0.8–1.0 mm long.

This little known species has been collected only a few times from the slopes of Cerro Horqueta and along the Bajo Chorro Trail, which are both in the vicinity of Boquete to the east of Volcán Chiriquí. The closest affinities of this species appear to be with *Burmeistera utleyi* which is known only from the Cerro Punta region to the west of Volcán Chiriquí and with *B. morii* from east of the Volcán and north of San Félix.

CHIRIQUÍ: Between Alto de las Palmas and top of Cerro de la Horqueta, 2100–2268 m, *Pittier* 3253 (US). Bajo Mono-Robalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4811* (MO). S slopes of Cerro Horqueta, N of Boquete, ca. 6000 ft, *Wilbur et al. 13467* (DUKE). SW slopes of Cerro Horqueta, ca. 6 km NW of Boquete, 1700–1800 m, *Wilbur et al. 15440* (DUKE).

5. **Burmeistera dukei** Wilbur.[6] TYPE: Panama, *Kirkbride & Duke 1295* (MO, holotype; DUKE, REED, isotypes).

Suffruticose sprawling *herbs*; branches puberulent. Principal *leaves* with blades elliptic, 4–15 cm long, 1.8–6.0 cm wide, ca. 2–3 times as long as wide, apically acute, basally cuneate, marginally shallowly and indistinctly repand with the slightly callose serrulations mostly 5–8 mm apart, glabrous on the upper surface, densely puberulent on the principal veins beneath; petioles 0.5–1.8 cm long, moderately to densely puberulous. *Flowers* 2.2–2.5 cm long; pedicels solitary in the upper leaf axils, spreading to ascendant, slender, moderately to densely puberulous, ebracteolate, 2.5–4 cm long; hypanthium in anthesis cylindric, spiculate to puberulous, basally acute, 4–5 mm long, 2.5–3.5 mm in diameter medially; calyx lobes oblong to lanceolate, acute to obtuse, denticulate, puberulent, 3.5–5 mm long, 2.5 mm wide; corolla moderately to densely puberulent, green, the tube 6–7 mm long and ca. 2.5 mm in diameter, the lobes linear to narrowly oblong, the upper lobe 9–11 mm long, the lateral lobes, 6–8 mm long, the lowermost lobe about 5 mm long; filament tube glabrous or sparingly puberulent, 20–22 mm long, the anthers externally glabrous, 3–4 mm long, the lowest anther lightly pilose-fringed. *Berries* (immature) red.

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[6] *Burmeistera dukei* Wilbur, sp. nov. Planta suffruticosa; ramuli puberuli. Lamina foliorum elliptica, 4–15 cm longa et 1.8–6.0 cm lata, 2–3-plo longiora quam lata, acuta ad apicem et basi cuneata, margine surrulata 1–2 serrulatis per cm; petioli puberuli, 0.5–1.8 cm longi. Flores 2.2–2.5 cm longi; pedicelli puberuli, 2.5–4 cm longi. Hypanthium cylindricum, spiculatum vel puberulum, 4–5 mm longum et 2.5–3.5 mm latum; lobi calycis lanceolati vel oblongi, denticulata, puberuli, 3.5–5 mm longi et ca. 2.5 mm lati. Corolla puberula, virenta; tubus 6–7 mm longus; lobi lineari vel oblongi, superiori 9–11 mm longi, laterali 6–8 mm longi et inferiori ca. 5 mm longi. Filamenta glabra vel sparsissime puberula, 20–22 mm longa; anthearum tubus glaber. Bacca immatura, rubra.

This species from Darién is known only from the type collection.

DARIÉN: Cuasi-Caná Trail between Cerro Campamiento and La Escalera to "Páramo" E of Tres Bocas, cloud forest and mossy forest, *Kirkbride & Duke 1295* (DUKE, MO, REED).

6. **Burmeistera glauca** (F. E. Wimmer) Gleason, Bull. Torrey Bot. Club 52: 98. 1925.

Centropogon glaucus F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 251. 1924. TYPE: Panama, *Pittier 3219* (US, holotype).

Epiphytic, suffrutescent, slender, glabrous *herbs*; stems hollow, to 70 cm long. *Leaves* with blades lanceolate to narrowly ovate, 2.7–5.0(–8.0) cm long, 1.2–2.5 cm wide, mostly 2–4 times as long as wide, glabrous, apically narrowed gradually to a long-acuminate, often falcate tip, basally rounded, marginally shallowly crenate-serrate with 2–4 callose-tipped teeth per cm; petioles 4–7 mm long, glabrous. *Flowers* 3–3.5 cm long; pedicels solitary in the upper leaf axils, spreading, usually stiff, glabrous, ebracteolate, 5–9 cm long; hypanthium in anthesis cylindric, basally rounded, flaring at the summit; calyx lobes deltoid or ovate, blunt, 1.5–2.5 (–3.5) mm long, marginally entire to callose-denticulate, glabrous, erect, green to purplish; corolla glabrous, greenish, purplish or russet red, the tube 15–18 mm long, basally little expanded, the lobes lanceolate, the 2 upper lobes 10–12 mm long, the two lateral lobes 6–8 mm long, the lowermost lobe 5–6 mm long; filament tube ca. 20 mm long, glabrous, basally distinct and adherent to the corolla tube, the anthers 3.5–5.5 mm long, the 2 shorter anthers apically densely fringed with white, pilose trichomes, otherwise all anthers glabrous. *Berries* much inflated, (2–)3–5 cm in diameter, 3–6 cm long, magenta, oblong-ovoid with a truncate apex; seeds fusiform or cylindric, light brown with dark apiculate tips, minutely foveate-reticulate, 0.9–1.2 mm long.

This species is known from the wet montane forests of Chiriquí Province at an elevation of about 1,700–2,500 m. It is known from both east and west of Volcán Chiriquí. Its bladdery, greatly inflated berry is strongly reminiscent of that of *Burmeistera vulgaris*.

BOCAS DEL TORO: Between Quebrada Menaco and Buena Vista on Chiriquí Trail, *Kirkbride & Duke 674* (MO). CHIRIQUÍ: Bajo Mono-Robalo Trail, W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4818* (MICH, MO). S flank of Cerro Horqueta along high trail to summit, 2100 m, *Cochrane 6275* (MO). Las Nubes, ca. 2000 m, *Croat 26455* (DUKE, MO). Bajo Chorro, 6000 ft, *Davidson 383* (F, GH, MO, US). NE ridge leading to Cerro Horqueta, 1800–1900 m, *Luteyn 3788* (DUKE). Ridge E of Cerro Horqueta, 1700–1900 m, *Luteyn & Wilbur 4620* (DUKE, MICH, MO). Cerro Pando at the Costa Rican-Panamanian border, 2000–2482 m, *Mori & Bolten 7282* (DUKE, MO). Cuestas de Las Palmas, S slopes of Cerro de la Horqueta, 1700–2100 m, *Pittier 3219* (US). Cerro Colorado, continental divide 50 km N of San Félix, 1400 m, *Mori & Dressler 7858* (DUKE, MO). N of San Félix at Chiriquí-Bocas del Toro border on Cerro Colorado, 5000–5500 ft, *Mori & Kallunki 5952* (DUKE, MO). Cerro Horqueta, 6500 ft, *von Hagen 2033* (MO). E of Guadeloupe along the Río Chiriquí Viejo, ca. 2 mi NE of Cerro Punta, 7000 ft, *Wilbur & Teeri 13104* (DUKE, F, GH, LL, MICH, MO, NY, US). Beyond Las Nubes, 7500 ft, *Wilbur & Teeri 13209* (DUKE, F, MICH, MO). S slopes of Cerro Horqueta N of Boquete, 6400–6600 ft, *Wilbur et al. 13450* (CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, US, WIS). 4 mi NW of Boquete, 6000 ft, *Wilbur et al. 13532* (DUKE, MICH, MO). Ridge leading to summit of Cerro Horqueta on southern slope, 6500–7500 ft, *Wilbur et al. 17309* (DUKE, CR, F, GH, LL, MICH, MO, NY,

PMA, US, WIS). Cerro Horqueta, 1500–1800 m, *Wilbur & Luteyn 19224, 19334* (both DUKE).

7. **Burmeistera kirkbridei** Wilbur.[7] TYPE: Panama, *Kirkbride & Duke 984* (MO, holotype).

Shrublets; stems terete, glabrous, purplish. Principal *leaves* with blades elliptic, 3.5–7 cm long, 1.5–3.5 cm wide, ca. 2–3 times as long as wide, apically acute to acuminate, basally cuneate, marginally indistinctly serrulate with ca. 2–4 callosities per cm, glabrous on both surfaces; petioles glabrous, 1.2–3 cm long. *Flowers* 1.2–1.5 cm long; pedicels solitary in the upper leaf axils, ascendant, slender, glabrous, ebracteolate, ca. 3 cm long; hypanthium in anthesis obconic, glabrous, basally acute, ca. 3 mm long, 3 mm in diameter; calyx lobes ovate or oblong-elliptic, acute, entire, glabrous, ca. 3.5 mm long, 1.5 mm wide; corolla densely but inconspicuously short-pubescent with spreading, stiff trichomes to 0.1 mm long, dark purplish and reportedly tipped with pink, the tube ca. 6 mm long, 2.5–3 mm in diameter, the lobes ovate with an acute to acuminate tip, the 2 upper lobes ca. 6 mm long, the 2 lateral lobes ca. 4 mm long, the lowermost lobe ca. 3 mm long; filament tube distally puberulent, ca. 7 mm long, the anthers all appressed puberulous externally, the longest anther ca. 2 mm long and the shortest ca. 1.5 mm long. *Fruits* and seeds unknown.

This species is known only from the holotype collected in the elfin forest at the divide separating the provinces of Bocas del Toro and Chiriquí, Panama. The flowers of *Burmeistera kirkbridei* are among the smallest known in the genus.

BOCAS DEL TORO-CHIRIQUÍ: Elfin forest on the Bocas del Toro-Chiriquí border at the divide on the Chiriquicito-Caldera Trail, *Kirkbride & Duke 984* (MO).

8. **Burmeistera microphylla** Donnell Smith, Bot. Gaz. (Crawfordsville) 25: 146. 1898. TYPE: Costa Rica, San José, La Palma, 1520 m, *Werckle 11600* (US, holotype).

?*Centropogon scandens* Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1857: 157. 1857. TYPE: Costa Rica, Jaris, *Oersted* (?C, not seen).

C. aurobarbatus F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 251. 1924. TYPE: Costa Rica, Heredia, Barba, *Brade 2315* (B, lectotype, not seen).

Burmeistera aurobarbata (F. E. Wimmer) F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 35. 1932.

B. aurobarbata var. *valde-cuspidata* Suessenguth, Bot. Jahr. Syst. 72: 287. 1942. TYPE: Costa Rica, Vara Blanca, *Kupper 256* (M, holotype; M, isotype).

B. aurobarbata var. *cuspidata* F. E. Wimmer, Pflanzenreich IV. 276b (Heft 69): 151. 1943. TYPE: Costa Rica, Cordillera Central and the vicinity of San Ramon (type not designated).

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[7] *Burmeistera kirkbridei* Wilbur, sp. nov. Planta suffruticosa. Rami tereti glabri. Lamina foliorum elliptica, 3.5–7 cm longa et 1.5–3.5 cm lata, circa 2–3-plo longiora quam lata, acuta vel acuminata, basi cuneata, margine serrulata 2–4 denticulis per cm; petioli glabri, 1.2–3.0 cm longi. Flores 1.2–1.5 cm longi; pedicelli glabri, ca. 3 cm longi. Hypanthium obconicum, glabrum; lobi calycis ovati vel oblong-elliptici, integri, glabri, ca. 3.5 mm longi et 1.5 mm lati. Corolla puberula, atro-violacea; tubus ca. 6 mm longus; lobi ovati, acuti vel acuminata, 3–6 mm longi.

Epiphytic, suffrutescent, glabrous *herbs*; stems pendent, hollow, (0.3–)0.9–1.5 m long. Principal *leaves* with blades variable in size and shape, elliptic to lanceolate, ovate or obovate, usually (1.3–)4–7(–12) cm long and 1.5–3(–4.5) cm wide, mostly 2–4(–6) times as long as wide, glabrous, thick and somewhat fleshy when fresh, coriaceous when dry, apically blunt, acute or acuminate, often with a slender, caudate tip to 2.5 cm long, basally rounded and abruptly contracted to gradually cuneate-tapering, marginally entire or indistinctly crenate-serrate with irregularly spaced callosities, dark green above, pale green beneath, sometimes tinged with purple; petioles 0.5–1.3 cm long, glabrous. *Flowers* (2.5–)3–4 cm long; pedicels solitary in the upper leaf axils, strongly ascendant, spreading or slightly deflexed, ebracteolate, (1.5–)2.5–4(–5.5) cm long; hypanthium in anthesis campanulate, basally narrowed and often long-tapering, glabrous, 5–7 mm long; calyx lobes linear, apically blunt, entire or obscurely callose-denticulate, erect to spreading or reflexed, (2–)4–10(–15) mm long, glabrous; corolla glabrous, pale cream to greenish tinged with russet red externally and creamy yellow internally, the tube (12–)15–20 mm long, the lobes lanceolate to broadly linear, the 2 upper lobes 8–11 mm long, the 2 lateral lobes 6–8 mm long, the lowest lobe only ca. 4 mm long; filament tube 18–27 mm long, glabrous or sparingly puberulent distally, the anthers (3–)4–5.5 mm long, externally with sparse to copious hirsutulous yellow trichomes 0.2–0.4 mm long, rarely glabrous, the 2 shorter anthers with a conspicuous tuft of wavy, pilose, soft yellow or rarely whitish? trichomes. *Berries* little inflated, 5–9(–12) mm in diameter, usually white to purplish tinted at maturity; seeds oblong, flattened, shallowly pitted, 1.2–1.5 mm long.

This species is a common epiphyte in the wet forests of the Costa Rican Cordillera Central but is not known south of the northern section of the Talamancas until it appears in the wet montane forests west of Cerro Punta and Volcán Chiriquí of Panama. It has not yet been collected between Chiriquí and Coclé, probably an indication of the incompleteness of botanical explorations.

There is considerable variation in leaf shape in this species as reflected in the above synonymy but the variation is morphologically continuous.

CANAL ZONE: Between Fort San Lorenzo and Fort Sherman, *Mori & Kallunki 2727* (MO). CHIRIQUÍ: Las Nubes, 2000 m, *Croat 26427A* (MO). 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Liesner 309* (DUKE). Trail beyond Las Nubes, midway between Cerro Punta and Cerro Picacho, NW of town of Cerro Punta, 1900–2200 m, *Luteyn & Wilbur 4624, 4632* (both DUKE). Las Nubes, 5 km NW of Cerro Pando, 6000–6500 ft, *Mori & Bolten 7235* (MO). Las Nubes region, 3–5.5 km NW of Cerro Punta and 2 km NW of Las Mirandes, 2000–2410 m, *Utley et al. 245* (DUKE, MICH). NW side of Cerro Punta beyond Las Nubes, 7500 ft, *Wilbur & Teeri 13210* (DUKE). Ca. 5 km NW of Cerro Punta, 2000–2300 m, *Wilbur et al. 15198* (DUKE, MO). Ridge near Las Nubes, ca. 7200 ft, *Wilbur & Almeda 17081* (DUKE); *Wilbur et al. 17106* (DUKE, MICH, MO). Ca. 5 km NW of Cerro Punta towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19392* (DUKE, F, MICH, MO, US). COCLÉ: Hills N of El Valle de Antón, 1000 m, *Allen 2343* (MO, US). Cerro Pajita, hills N of El Valle de Antón, 1000–1200 m, *Allen 4180* (MO). La Mesa above El Valle de Antón, *Croat 14396* (MO). El Valle, 800–1000 m, *Duke 13229* (MO). Cerro Pilón, El Valle, 3000 ft, *Duke & Lallathin 14978* (MO). Mountains N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1725* (MO). PANAMÁ: Cerro Jefe, ca. 1000 m, *Mori & Kallunki 3625, 3799* (both DUKE, MO); *Mori 7984* (MO). El Llano-Cartí road, 10.5 km N of El Llano, 450 m, *Nee 10524* (MO).

9. **Burmeistera morii** Wilbur.[8] TYPE: Panama, *Mori & Kallunki 5951* (DUKE, holotype; MO, isotype).

Epiphytic suffrutescent *herbs* ca. 50 cm tall; stems glabrate. Principal *leaves* with blades elliptic, (5–)8–10.5 cm long, (2.0–)3.0–4.2 cm wide, mostly 2.5–3 times as long as wide, apically acute to acuminate, basally cunneate, marginally repand-denticulate with ca. 3 to 5 inconspicuous callosities per cm, glabrous above and beneath, with strongly arching, conspicuous secondary veins rejoining just within the margins; petioles 1.0–1.5 cm long, glabrous. *Flowers* ca. 2.8 cm long; pedicels solitary in the upper leaf axils, spreading to strongly ascendant, glabrous, ebracteolate, 4–6 cm long but elongating in fruit to at least 9 cm; hypanthium at anthesis shortly turbinate, glabrous, basally acute and with divergent sides, 3–6 mm long, 3–4 mm in diameter at its summit; calyx lobes oblong, obtuse, entire, glabrous, 3–4 mm long; corolla glabrous to inconspicuously spiculate, green, the tube 12–14 mm long, 1.5–2 mm in diameter, the lobes falcate, narrowly oblong, acute, the 2 upper lobes 10–12 mm long, the 2 lateral lobes 6–8 mm long, the lowermost lobe 3–4 mm long; filament tube slightly exserted, 20–22 mm long, glabrous, the anthers 2.5–5 mm long, externally puberulous, the 2 shorter anthers with a thin, apical fringe of trichomes. *Berries* pinkish, noninflated, subglobose, ca. 7 mm high, 8 mm in diameter at the apex.

This species is known only from the type. Its closest relatives appear to be *Burmeistera dendrophila* and *B. utleyi*. The species is distinctive in its small flowers and in the foliar venation which is reminiscent of *B. parviflora*.

CHIRIQUÍ: N of San Félix at Chiriquí-Bocas del Toro border, on Cerro Colorado coppermine road along continental divide, lower montane cloud forest, 5000–5500 ft, *Mori & Kallunki 5951* (DUKE, MO).

10. **Burmeistera panamensis** Wilbur.[9] TYPE: Panama, *Duke 6081* (MO).

Shrublets; branchlets sparingly appressed-pubescent. Principal *leaves* with blades broadly elliptic to oblong, 15–22 cm long, 7–9 cm wide, ca. 2.5 times as long as wide, apically acute and basally broadly rounded, marginally subentire

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[8] *Burmeistera morii* Wilbur, sp. nov. Planta suffruticosa, epiphytica, ca. 50 cm alta. Lamina foliorum elliptica, (5–)8–10.5 cm longa and (2.0–)3.0–4.2 cm lata, glabra. Flores ca. 2.8 cm longi; pedicelli glabri, 4–6 cm longi. Hypanthia turbinata, glabra, 3–6 mm longa; lobi calycis oblongi, obtusi, integri, glabri, 3–4 mm longi. Corolla glabra, viridis; tubi 12–14 mm longi et 1.5–2 mm lati; lobi superiores 10–12 mm longi, laterales 6–8 mm longi et inferiores 3–4 mm longi. Filamenta glabra, exserta, 20–22 mm longa; antherae puberulae, 2.5–5 mm longae, orificio ciliatae.

[9] *Burmeistera panamensis* Wilbur, sp. nov. Planta suffruticosa; ramuli sparse appressi-pubescenti. Lamina foliorum elliptica vel oblonga, 15–22 cm longa et 7–9 cm lata, ca. 2.5-plo longiora quam lata, acuta ad apicem et basi rotundata, margine subintegra; petioli appressi-pubescens, ca. 1 cm longi et 2 mm in diametro. Flores ca. 4.8 cm longi; pedicelli appressi-pubescens, ca. 6 cm longi. Hypanthium cylindricum vel campanulatum, glabrum vel sparse appressi-pubescens, 7–9 cm longum et 5–7 mm in diametro; lobi calycis lineari, integra vel subintegra, glabri, 12–15 mm longi et 2–2.5 mm lati. Corolla glabra, virenta; tubus circa 25 mm longus et 4–6 mm in diametro; lobi lineari et oblongi, superiori 14–17 mm longi et 4–5 mm lati, laterali ca. 11 mm longi et inferiori 8–9 mm longi. Filamenta glabra, ca. 33 mm longa; anthearum tubus glaber externale sed anthearum inferiores apice villoso-barbatea. Bacca globosa, ca. 15–18 mm diametro.

or inconspicuously dentate with 1–2 low teeth per cm, inconspicuously appressed pubescent especially on the veins on both the upper and lower surfaces; petioles stout, ca. 1 cm long, 2 mm in diameter, sparingly appressed pubescent. *Flowers* ca. 4.8 cm long; pedicels slender, solitary in the upper leaf axils, arching to ascendant, ebracteolate, ca. 6 cm long; hypanthium in anthesis campanulate to cylindric, 7–9 mm long, 5–7 mm in diameter, glabrous to sparingly appressed pubescent; calyx lobes 12–15 mm long, 2–2.5 mm wide, obtuse, entire to inconspicuously denticulate; corolla glabrous, greenish, the tube ca. 25 mm long, basally ca. 4 mm in diameter, gradually flaring above to ca. 6 mm in diameter, the lobes narrowly linear-oblong, falcate, the 2 upper lobes 14–17 mm long and 4–5 mm wide, the 2 lateral lobes ca. 11 mm long, the lowermost lobe 8–9 mm long; filament tube ca. 33 mm long, glabrous throughout, the longer anthers ca. 8 mm long, the shorter anthers ca. 5 mm long, all anthers externally glabrous, the 2 lowermost apically densely pilose with whitish trichomes 2.0–2.2 mm long. *Berries* globose or subglobose, 15–18 mm in diameter; seeds fusiform, ca. 0.8 mm long.

DARIÉN: Cloud forest, Cerro Pirre, *Duke 6081* (MO). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13835* (MO, in part).

11. **Burmeistera parviflora** F. E. Wimmer ex Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1408. 1938. TYPE: Costa Rica, Prov. de Alajuela, Cerros de San Antonio de San Ramón, 1100 m, *Brenes 5636* (F).

Epiphytic or terrestrial, suffrutescent *herbs*; stems hollow, 30–50(–100) cm high, glabrous or sparingly to moderately puberulous above. Principal *leaves* with blades elliptic, oblong or ovate, 6.5–12 cm long, (1.5–)2.5–4(–5) cm wide, usually 2.5–3.5 times as long as wide, apically abruptly narrowed to an acuminate tip (0.5–)1–2 cm long, basally cuneate to somewhat rounded, marginally shallowly crenate-serrulate with 4–6(–10) callose-tipped teeth per cm and with a prominent submarginal vein extending the length of the blade, sparsely to densely but microscopically papillate or strigillose especially on the veins beneath but appearing glabrate; petioles 1–3 cm long, glabrous or minutely puberulous. *Flowers* 2–2.5 cm long; pedicels solitary in the upper leaf axils, spreading-ascending, somewhat flexuous, slender, glabrous, ebracteolate, 4–9 cm long; hypanthium in anthesis glabrous, obconic, basally subacute, pale green to dark reddish purple, 3–6 mm long; calyx lobes acutely to bluntly triangular, 2–3(–4) mm long, glabrous, entire or with a few inconspicuous marginal callosities, dark red or purplish, erect or somewhat spreading; corolla glabrous, clear yellow, the tube (5–)7–14 mm long, the lobes lance-ovate, the 2 upper lobes 5–9 mm long, the lateral lobes (3–)5–8 mm long, the lowest lobe 3–5 mm long; filament tube 12–19 mm long, distally puberulent, glabrous below, the filaments not adnate to the corolla tube, the 3 upper anthers glabrous and ca. 4 mm long, the 2 shorter or lower anthers ca. 2.5 mm long, with a scanty fringe of soft white hairs. *Berries* scarcely inflated, obovoid, 5–6 mm in diameter, pinkish to white; seeds light brownish, oblongish, 0.8–1.0 mm long, shallowly pitted with depressions slightly longer than wide.

This species occurs in mountain forests in Chiriquí and also in Costa Rica between 1,100–2,700 m.

CHIRIQUÍ: Cerro Pando at the Costa Rican-Panamanian border between 2000–2482 m, *Mori & Bolten 7279* (DUKE, MO).

12. **Burmeistera pirrensis** Wilbur.[10] TYPE: Panama, *Gentry & Clewell 7084* (DUKE, holotype; MO, isotype).

Suffruticose terrestrial or epiphytic *herbs*; branches sparingly to densely puperulous. Principal *leaves* with blades elliptic to ovate, 8–15 cm long, 3.5–7.0 cm wide, ca. 2–2.5 times as long as wide, apically acute, basally cuneate to broadly rounded, marginally appearing entire but indistinctly repand-serrulate with 1–3 callose serrulations per cm, glabrate above with a few, scattered trichomes in the median groove, moderately to densely puberulent on the principal veins beneath; petioles puberulous, 1.5–3 cm long. *Flowers* 2–2.5 cm long; pedicels solitary in the upper leaf axils, erect to ascendant, slender, glabrous, ebracteolate, 2–3 cm long; hypanthium in anthesis cylindric to somewhat obconic, glabrous, basally acute, ca. 5 mm long, 3 mm in diameter; calyx lobes ovate to oblong, obtuse, entire, glabrous, 1.5–2.5 mm long, ca. 1–1.5 mm wide; corolla glabrous, greenish, the tube 10–13(–15) mm long, ca. 2.5 mm in diameter, the lobes narrowly oblong to ovate-oblong, the upper lobes 9–11 mm long, the lateral lobes ca. 7 mm long, the lowermost lobe 5–6 mm long; filament tube inconspicuously and finely puberulous, 22–25 mm long, the anthers externally sparingly to moderately puberulous, the two lowermost with a thin pilose fringe. *Berries* globose, ca. 6 mm in diameter, white.

With four different collections, this species is the best represented and hence best known of the *Burmeistera* species found in the Province of Darién.

DARIÉN: Ascent of Cerro Pirre, S of El Real, 750–1030 m, *Duke 5350* (MO). Between Upper Río Membrillo and Camp 7 on the Construction Road to San Blas, 100–800 m, *Duke 10890* (MO). Cerro Pirre, 2500–4500 ft, *Duke & Elias 13836, 13791* (both MO). Cloud forest, summit of Cerro Pirre, 1000–1400 m, *Gentry & Clewell 7084* (DUKE, MO).

13. **Burmeistera tenuiflora** Donnell Smith, Bot. Gaz. (Crawfordsville) 25: 147. 1898. TYPE: Costa Rica, Prov. de Heredia, Volcán Barba, *Pittier 19* (US, holotype; CR, isotype).

Epiphytic or terrestrial (?), suffrutescent *herbs*; stems (0.7–)1–2.5 m long, glabrous or pubescent above. Principal *leaves* with blades elliptic to oblong, 5–16 cm long, 2.5–5.5 cm wide, mostly ca. 3 times as long as wide, apically acuminate, basally rounded to subacute, marginally subentire or sinuate and obscurely denticulate, glabrous above, beneath glaucous and short-pubescent on the veins with

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[10] *Burmeistera pirrensis* Wilbur, sp. nov. Planta suffruticosa, terrestris vel epiphytica; ramuli puberuli. Lamina foliorum elliptica vel ovata, 8–15 cm longa et 3.5–7 cm lata, ca. 2–2.5-plo longiora quam lata, acuta ad apicem et basi cuneata vel rotundata, margine repand-serrulata, 1–3 calloso-serrulatis per cm, nervis subtus puberulis; petioli puberuli, 1.5–3 cm longi. Flores 2–2.5 cm longi; pedicelli glabri, 2–3 cm longi. Hypanthia cylindrica vel obconica, glabra, ca. 5 mm longa et 3 mm lata; lobi calycis ovati vel oblongi, obtusi, integri, glabri, 1.5–2.5 mm longi et 1–1.5 mm lati. Corolla glabra, virenta; tubus 10–13(–15) mm longus et ca. 2.5 mm latus; lobi oblongi vel ovato-oblongi; lobi superiori 9–11 mm longi, laterali ca. 7 mm longi et inferiori ca. 5 mm longi. Filamenta puberula, 22–25 mm longa; antherarum tubus puberulus. Bacca globosa, alba, ca. 6 mm longa et lata.

appressed to strongly spreading hyaline to tawny trichomes 0.1–0.3 mm long; petioles short-pubescent, 0.5–1 cm long. *Flowers* ca. 4 cm long; pedicels solitary in the upper leaf axils, glabrous, spreading to ascendant, stiff, ebracteolate, 4.5–8 cm long; hypanthium in anthesis narrowly turbinate or obconic, basally acute and long-attenuate, glabrous; calyx lobes linear with a blunt tip, entire or inconspicuously callose-denticulate, glabrous, (7–)11–20 mm long; corolla glabrous or sparsely pubescent externally, greenish or yellowish white, the tube 11–15 mm long, broadest basally and distally, the lobes falcate, the upper lobe 9–10 mm long, the 3 lower lobes ca. 7 mm long; filament tube ca. 2.2 cm long, distally pubescent and otherwise glabrous, basally distinct and completely free from the corolla tube, the upper anthers 5.5–6 mm long, sparsely pilose apically, all anthers sparsely short-pubescent at the base and on the back. *Berries* little inflated, obovoid, 7–10 mm long, 5 mm in diameter, basally acute; seeds oblong.

This species is known from the Cordillera de Tilarán and the Cordillera Central of Costa Rica and in Panama from both the Boquete region and also near Santa Fé de Veraguas. These discontinuities are probably due to incomplete collecting.

BOCAS DEL TORO: Cerro Horqueta, 6000–7000 ft, *Allen 4951* (MO). CHIRIQUÍ: Bajo Chorro, 6000 ft, *Davidson 79* (F, GH, US). N of San Félix on Cerro Colorado coppermine road, 5000–5500 ft, *Mori & Kallunki 5829* (DUKE, MO). SW slopes of Cerro Horqueta, ca. 6 km NW of Boquete, 1700–1800 m, *Wilbur et al. 15439* (DUKE, MO). S slope of Cerro Horqueta, 6500–7500 ft, *Wilbur et al. 17305* (DUKE). PANAMÁ: Cerro Jefe, 1000 m, *Mori & Kallunki 3796* (MO). VERAGUAS: Cerro Tute, vic. of Santa Fé, 3000 ft, *Allen 4346* (MICH, in part). Río Primero Brazo, 2.5 km beyond Agriculture School near Santa Fé, 700–750 m, *Croat 25488* (MO). Road between Escuela Agrícola and Alto Piedra and Río Dos Bocas, 730–770 m, *Croat 25959* (MO). 12–15 km NW of Santa Fé, 650–750 m, *Dressler 4825, 5007* (both DUKE). Above Río Primero Brazo, 5 mi NW of Santa Fé, 700–1200 m, *Liesner 803* (MO). NW of Santa Fé, 8.8 km from Escuela Agrícola, *Mori & Kallunki 3249* (MO); *Mori et al. 3959* (MO). Cerro Tute, ca. 5 km NW of Santa Fé, 1100–1400 m, *Mori et al. 7596* (MO). 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3249* (DUKE, MO), *3959, 6166* (both DUKE). Cerro Tute, ca. 10 km NW of Santa Fé, *Mori 6758* (DUKE, MO). Ca. 2 km N of Santa Fé, *Wilbur & Luteyn 19108* (DUKE, MICH).

14. **Burmeistera toroensis** Wilbur.[11] TYPE: Panama, *Kirkbride & Duke 983* (MO, holotype).

Suffrutescent *herbs*; stems purplish, glabrous throughout. Principal *leaves* with blades apparently somewhat thickened or fleshy, elliptic, 4–7.5 cm long, 1.5–2.7 cm wide or ca. 2.5–3 times as long as wide, apically acute to acuminate, basally acutely tapering, marginally with a slightly thickened border and entire or obscurely serrulate with 1–2(–4) slightly incurved, callose-tipped serrulations per cm, both surfaces glabrous; petioles 6–9 mm long. *Flowers* 3(–4?) cm long; pedicels solitary in the upper leaf axils, straight, divergent, glabrous, ebracteolate,

[11] *Burmeistera toroensis* Wilbur, sp. nov. Planta suffruticosa; rami tereti glabri. Lamina foliorum elliptica, 4–7.5 cm longa et 1.5–2.7 cm lata, ca. 2.5–3-plo longiora quam lata, acuta, basi cuneata, margine subintegra remote calloso-serrulata 1–2(–4) denticulis per cm, glabra; petioli 6–9 mm longi, glabri. Flores 3 cm longi; pedicelli glabri, ca. 5 cm longi. Hypanthium obconicum, glabrum, 6 mm longum; lobi calycis erecti, ovati, integri, glabri, obtusi, 6 mm longi. Corolla glabra, atro-violacea; tubus ca. 13–15 mm longus; lobi lance-oblongi, acuti, 2 superiores 7 mm longi. Filamenta glabra; tubus antherarum glaber.

ca. 5 cm long; hypanthium obconic to somewhat cylindric, glabrous, basally acute, 6 mm long; calyx lobes erect, ovate, obtuse, entire, glabrous, 1–1.5 mm long; corolla glabrous, purplish, the tube 13–15 mm long, the lobes lance-oblong, acute, the 2 upper lobes 7 mm long, the 2 lateral lobes about 5 mm long, the lowermost lobe not seen; filament tube immature, glabrous, the anthers externally glabrous with an apical fringe of short white trichomes. *Fruits* unknown.

This species is known only from the type collection.

BOCAS DEL TORO-CHIRIQUÍ: Elfin forest at divide on Chiriquicito-Caldera Trail, *Kirkbride & Duke 983* (MO).

15. **Burmeistera utleyi** Wilbur.[12] TYPE: Panama, *Wilbur et al. 15222* (DUKE, holotype; MICH, isotype).

Epiphytic *shrublets* or suffrutescent *herbs*, 60–150 cm long; stems short-pubescent above with densely spreading hairs, glabrescent below with the tawny trichomes 0.1–0.2 mm long. Principal *leaves* with blades elliptic to less commonly ovate to obovate, 6–12.5 cm long, mostly 2–4 times as long as wide, apically acute to acuminate or obtuse, basally acutely tapering, marginally appearing subentire but actually with 1–2 indistinct callosities per cm, glabrous above to moderately puberulent in the basal portion of the midvein, densely short-pubescent beneath especially on the veins with tawny spreading trichomes ca. 0.1 mm long, the venation pinnate with the lateral veins forming a vein ca. 1 mm from the margin; petioles 1–3 cm long, densely spreading short-pubescent. *Flowers* 4–5 cm long; pedicels solitary in the upper leaf axils, straight to curving, moderately to densely spreading, short-pubescent, ebracteolate, (5–)8–12 cm long; hypanthia at anthesis obconic, moderately to densely short-pubescent, the spreading trichomes ca. 0.1 mm long, basally acute, 5–9 mm long and distally 3–7 mm in diameter, vertically nerved or ridged; calyx lobes oblong to ovate, obtuse, entire, inconspicuously short-pubescent, 1.5–3 mm long; corollas moderately but inconspicuously spreading-short-pubescent, light green or green with purplish lines, the tube 14–18 mm long, the lobes falcately oblong to ovate, acute to acuminate, the 2 upper lobes 12–16 mm long, the 2 lateral lobes 8–11 mm long, the lowermost lobe 4–6 mm long; filament tube exserted, 32–36 mm long, proximally glabrous, distally slightly puberulous to glabrous, the anthers 3–6 mm long, externally slightly puberulous, apically glabrous or sparsely pubescent. *Fruits* and seeds unknown.

This species most closely resembles *Burmeistera dendrophila*. *Burmeistera utleyi*, known only from the area west of Volcán Chiriquí, differs from *B. dendrophila*, known only from the Boquete region east of Volcán Chiriquí, in hav-

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[12] *Burmeistera utleyi* Wilbur, sp. nov. Planta suffruticosa, terrestris vel epiphytica, 60–150 cm longa. Lamina foliorum elliptica vel raro ovata ad obovata, 6–12.5 cm longa et 2.5–5 cm lata, supra glabra et infra dense pubescens. Flores 4–5 cm longi; pedicelli puberuli, (5–)8–12 cm longi. Hypanthia obconica, puberula (trichoma patula, circa 0.1 mm longa); lobi calycis oblongi vel ovati, obtusi, integri, pubescenti, 1.5–3 mm longi. Corolla puberula, virenta vel virenta et violacea; lobi superior 12–16 mm longi, lobi lateralis 8–11 mm longi et lobus inferior 4–6 cm longus. Filamenta ± glabra, exserta, 32–36 mm longa.

ing densely spreading short-pubescent pedicels and hypanthia while the latter species has either glabrous or moderately spiculate or appressed short-pubescent pedicels and hypanthia.

CHIRIQUÍ: Las Nubes, ca. 2000 m, *Croat 26478* (MO). Vic. of Las Nubes, 2.7 mi NW of Río Chiriquí Viejo, 2200 m, *Croat 22405* (MO). Cerro Pando at the Costa Rican-Panamanian border, 2000–2482 m, *Mori & Bolten 7270* (MO). Las Nubes region, 3–5.5 km NW of Cerro Punta and 2 km NW of Las Mirandes, 2000–2410 m, *Utley et al. 243* (DUKE). 1 km N of Las Nubes and 5 km NW of the town of Cerro Punta, 2000–2300 m, *Wilbur et al. 15222* (DUKE, MICH). W of Las Nubes, ca. 5 km NW of Cerro Punta towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19356* (DUKE).

16. **Burmeistera vulgaris** F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 27, *pl. 123, fig. 14.* 1932. TYPE: Costa Rica, Prov. de San José, N of El Copey, *Standley 42686* (F, holotype; F, US, isotypes).—FIG. 1.

B. macrocalyx F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 19, *pl. 124.* 1932. TYPE: Costa Rica, *Wendland 839* (B, not seen).

B. pittieri F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 19, *pl. 124, fig. 20a.* 1932. TYPE: Costa Rica, Prov. de Cartago, Volcán Turrialba, *Pittier 7531* (B, W, syntypes, neither seen; GH, US, isosyntypes).

B. pittieri var. *decorans* F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 30: 19, *pl. 124, fig. 20b.* 1932. TYPE: Costa Rica, Prov. de San José, La Palma, *Tonduz* (Herb. Inst. Nat. Costaric. *12522*) (US, holotype).

Terrestrial or rarely epiphytic suffrutescent *herbs* or bushy *shrublets*; stems hollow, glabrous, 1–3(–4.5) m tall. Principal *leaves* with blades usually elliptic, 5–15 cm long, (1.5–)2.5–4.8 cm wide, mostly 2.5–5 times as long as wide, apically abruptly narrowed to a broad acuminate tip, basally rounded to gradually tapering, marginally sinuate with low teeth and 3–5 callosities per cm, glabrous above and beneath except for the often minutely scaberulous-puberulent veins; petioles slender, glabrous to inconspicuously puberulous, 1.3–2.0(–3.0) cm long. *Flowers* 4.5–5 cm long; pedicels solitary in the upper leaf axils, appressed to widespreading, occasionally flexuous, glabrous, ebracteolate, 7–10(–17) cm long; hypanthium in anthesis cylindric or slightly narrowed apically and basally rounded to subacute, 8–12 mm long, 4–5 mm in diameter, ca. 1.5–2 times as long as wide; calyx lobes extremely variable, narrowly triangular, blunt, apically rounded or subacute, prominently crenate, callose-denticulate to almost entire, ascendant to spreading, 4.5–12 mm long, often foliaceous and then broadly elliptic to oblong, coarsely toothed and (15–)20–28 mm long and 3–7 mm wide; corolla glabrous, pale green, the tube 12–16 mm long, basally somewhat inflated, the lobes oblong-falcate, the 2 upper lobes 10–18(–23) mm long, the lateral lobes 9–12 mm long, the lowest lobe 5–10 mm long; filament tube 26–32 mm long, distally glabrous to sparingly and inconspicuously puberulent, glabrous beneath, basally distinct but united to the corolla tube, the longer anthers 8–9 mm long, the shorter anthers ca. 5 mm long, all anthers glabrous except sometimes for a few, soft, white apical hairs. *Berries* much inflated, (2.0–)2.5–4.0 cm in diameter, 2.5–5.0 cm long; seeds linear-fusiform, 0.6–0.8 mm long, light brown with darker tips, minutely foveate-reticulate.

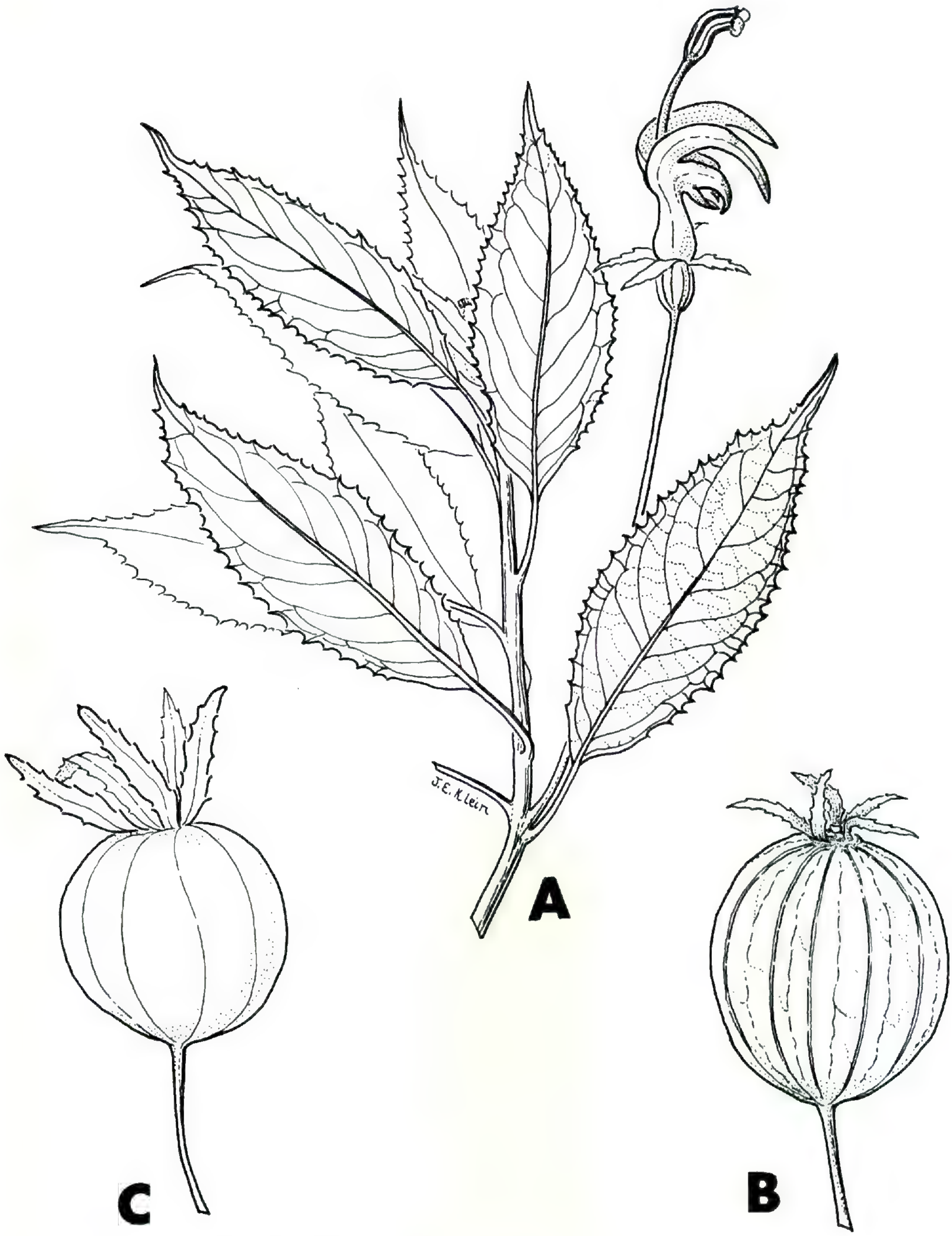

FIGURE 1. *Burmeisteria vulgaris* F. E. Wimmer.—A. Habit (×9/10).—B. Fruit (×9/10). [After *Wilbur & Teeri 13198* (MO).]—C. Fruit (×9/10). [After *Wilbur et al. 17252* (MO).]

This species occurs in wet forests in Costa Rica and western Panama, mostly at elevations of 1,200–2,550 m and in northwestern South America from Colombia and Ecuador.

The variability of the size of the calyx lobes of this species is most striking

and has been the principal feature emphasized by Wimmer in recognizing the several species and varieties listed in the synonymy of this species. The more numerous specimens now available confirm McVaugh's (1943) treatment of these taxa as a morphological continuum. The following names range from the smallest calyx lobes to the largest: *B. vulgaris*, *pittieri*, *pittieri* var. *decorans*, and *macrocalyx*.

BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4952* (MICH, MO). CHIRIQUÍ: Bajo Chorro, 6000 ft, *Davidson 378* (F, US). Bajo Chorro, 7000 ft, *Davidson 720* (F, US). Above Las Nubes, NW of Cerro Punta, 1900–2100 m, *Luteyn 3801* (DUKE, MO). Bajo Chorro trail, 2360–2500 m, *Luteyn 3827* (DUKE). Las Nubes, 5 km NW of Cerro Pando, 6000–6500 ft, *Mori & Bolten 7222* (DUKE, MO). Cerro Colorado on continental divide, 50 km N of San Félix, 1400 m, *Mori & Dressler 7763* (DUKE, MO). Las Nubes region, 3–5.5 km NW of Cerro Punta, 2000–2410 m, *Utley et al. 242, 249* (both DUKE, MICH). Beyond Las Nubes, 7500 ft, *Wilbur & Teeri 13198* (CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, US, WIS). Vic. of Las Nubes, 6000–7200 ft, *Wilbur et al. 17083* (DUKE, F, LL, MICH, MO, PMA, US). Vic. of Las Nubes, ca. 6 km NW of Cerro Punta, 7200 ft, *Wilbur et al. 17162* (DUKE). Boquete-Cerro Punta trail on the Boquete side of the pass, 8200 ft, *Wilbur et al. 17252* (DUKE, F, MICH, MO, PMA).

2. CENTROPOGON

Centropogon Presl, Prodr. Monogr. Lobel. 48. 1836. TYPE: *C. surinamensis* (L.) Presl = *C. cornutus* (L.) Druce.

Herbs or straggly, often sprawling, suffrutescent perennials or *shrubs*. *Leaves* simple, exstipulate, alternate, petiolate, pinnately veined and usually denticulate or serrulate. *Flowers* axillary in the upper leaves or reduced bracts and borne on usually bibracteolate pedicels; corolla purplish, red to pink, orange or rarely yellow or greenish white, the tube straight or curved, never dorsally cleft, rarely fenestrate, basally often strikingly contracted and commonly somewhat inflated above; filaments distinct below, basally adherent to the constricted basal portion or the corolla tube, monadelphous above, the anther tube with the opening usually partially closed by the incurved tips of the 3 longer or apparently adaxial anthers, the 2 shorter or apparently abaxial anthers bearing a tuft of stiff, white trichomes, these hairs sometimes in part concrescent into a cartilaginous, triangular, scale-like appendage; corolla, stamens and the nonarticulate style often tardily deciduous; ovary apically more or less truncate. *Fruits* berrylike, globose to somewhat cylindric, leathery or fleshy; seeds numerous, lenticular, 0.5–0.7 mm long, minutely foveate-reticulate, the reticulations more or less isodiametric.

This is a large genus of perhaps 225 species ranging from southern Mexico and the Lesser Antilles throughout much of Andean South America. Perhaps 40% of the more than 200 species of *Centropogon* occur in Colombia. Ecuador and Peru each has more than 50 species within its borders. Twenty-two species are known from Central America, here considered to include Panama, with 14 in Costa Rica and 12 in Panama. Six species occur in both Costa Rica and Panama. Seven species are endemic to Costa Rica and five are known only from Panama.

The genus is divisible into two major groups which apparently are natural, although Bentham, who first formally separated them, thought otherwise. They are treated here as the subgenera *Centropogon* and *Siphocampyloides* (Benth.

& Hook.) Wilbur. Subgenus *Centropogon* is readily separable by the cornute anthers which have a triangular scale composed of concrescent trichomes borne at the apex of the two lowermost anthers. This scale is absent in subgen. *Siphocampyloides*. McVaugh (1949) on the other hand recognized subgen. *Siphocampyloides* as a section along with three other sections. However, utilization of subgeneric categories better reflects the basic dichotomy in the genus. This does result in placing McVaugh's sects. *Siphocampyloides*, *Wimmeriopsis* and *Burmeisteroides* in the one subgen. *Siphocampyloides*, in spite of McVaugh's conclusion that they are "an agglomeration of several species-groups which have little in common." The probable monophyletic nature of the cornute-anthered species is, however, more impressive than the suggested polyphyletic origin of the noncornute taxa assembled in subgen. *Siphocampyloides*.

Literature:

McVaugh, R. 1940. Campanulaceae (Lobelioideae). *In* R. E. Woodson, Jr. & R. W. Schery. Contributions toward a flora of Panama. Ann. Missouri Bot. Gard. 27: 347–353.

———. 1949. Studies in South America Lobelioideae (Campanulaceae) with special reference to Colombian species. Brittonia 6: 450–493.

Wilbur, R. L. 1976. A synopsis of the Costa Rican species of the genus *Centropogon* (Campanulaceae, Lobelioideae). Brenesia 8: 59–84.

a. Two shorter anthers cornute, i.e., appendaged at the tip with a triangular scale of concrescent trichomes (Subgen. *Centropogon*).
  b. Flowers solitary in the axils of the relatively unreduced upper leaves; corolla glabrous, sometimes sparingly pilose or short-pubescent on the veins and the margins of the lobes but otherwise glabrous ..... 3. *C. cornutus*
  bb. Flowers clustered in terminal, corymbiform or racemose clusters borne in the axils of bracts or obviously reduced leaves; corolla typically short-pubescent or papillate in part or throughout, occasionally glabrous.
    c. Scandent, sprawling or arching, suffrutescent herbs; inflorescences pendent; anther tube with trichomes on the connectives mostly 2–3 mm long; corolla lobes yellowish to orange and contrasting greatly in color with the tube ..... 7. *C. granulosus*
    cc. Erect shrubs or suffrutescent herbs; inflorescences erect; anther tube glabrous or with trichomes on the connectives less than 1.2 mm long; corolla lobes not colored strikingly different than the tube, either pink, purplish or red.
      d. Corolla moderately to densely beset with slender-based trichomes less than 0.2 mm long; venation on the lower surface of the leaves with slender trichomes about 1 mm long; leaf margins doubly serrate ..... 2. *C. congestus*
      dd. Corolla densely beset with broadly based, conical, stiff projections 0.1–0.2 mm long; venation on the lower surface of the leaves glabrous (or very sparingly strigillose) or densely but microscopically granular-papillate; leaf margins appearing entire, indistinctly crenate-serrulate, or microscopically denticulate.
        e. Leaves fleshy and leathery when fresh, coriaceous or chartaceous when dry; venation of the lower leaf-surface densely but microscopically grandular-papillate; bracteoles 2–4 mm long; anther tube densely bearded in the commissures between the anthers ..... 11. *C. panamensis*
        ee. Leaves membranous when fresh, thinly membranous when dry; venation of the lower leaf-surface either glabrous or sparingly strigillose; bracteoles less than 1.2 mm long; anther tube glabrous or sparsely

strigillose; bracteoles less than 1.2 mm long; anther tube glabrous or sparsely strigillose ..... 4. *C. darienensis*

aa. Two shorter anthers with an apical, penicillate fringe of stiff trichomes and lacking a triangular, scalelike appendage of concrescent trichomes (Subgen. *Siphocampyloides*).
f. Inflorescences, upper stems, and the lower surfaces of the leaves bearing conspicuously branched, dendritic trichomes (Sect. *Siphocampyloides*) ..... 5. *C. ferrugineus*
ff. Inflorescences, upper stems, and the lower surfaces of the leaves glabrous or bearing only unbranched trichomes.
g. Corolla pale greenish-white, creamy, or greenish-yellow, scurfy-textured, lacking well-defined trichomes but the surface not smooth; corolla lobes equaling or longer than the tube; anther tube 13–15 mm long (Sect. *Burmeisteroides* ..... 12. *C. smithii*
gg. Corolla reddish or orange, either pubescent with obviously defined trichomes or glabrous; corolla lobes shorter than the tube, usually less than half as long; anther tube 10 mm long or less (Sect. *Wimmeriopsis*).
h. Filament tube (measured from base of anther tube to base of corolla) 4.8 cm long or longer.
i. Calyx lobes less than 6 mm long; bracteoles 3 mm long or less; corolla puberulent with trichomes less than 0.2 mm long, the lobes lacking a conspicuous corolline fringe of appendages ..... 6. *C. floricomus*
ii. Calyx lobes more than 6 mm long; bracteoles 6 mm long or longer; corolla with trichomes ca. 0.5 mm long, the lobes with conspicuous corolline appendages 1.0–1.7 mm long ..... 8. *C. gutierrezii*
hh. Filament tube 4.5 cm long or less.
j. Filament tube terminating 35 mm or more above the base of the corolla tube; corolla tube 35 mm long or longer; pedicels with bracteoles 1–4 mm long ..... 1. *C. coccineus*
jj. Filament tube terminating less than 35 mm (usually 32 mm or less) above the base of the corolla tube; corolla tube 30 mm long or less; pedicels ebracteolate.
k. Leaf blades narrowly lanceolate, mostly 3–6 times as long as wide, shallowly serrate, usually 1–2 cm wide ..... 9. *C. leucocarpus*
kk. Leaf blades ovate to lance-ovate, mostly 1.5–2.5 times as long as wide, dentate, mostly 2–4 cm wide ..... 10. *C. luteynii*

1. **Centropogon coccineus** (Hook.) Regel ex B. D. Jackson, Index Kew. 1: 479. 1893.—FIG. 2.

Siphocampylus coccineus Hook., Bot. Mag. 71: *tab. 4178*. 1845. Based on plants grown from seed at first allegedly collected by William Lobb in the Organ Mountains of Brazil but later corrected (Paxton's Mag. Bot. 12: 173. 1846.) to "shady places on the banks of the River Chagres, in New Grenada [Panama]."

S. *radicans* Kuntze, Rev. Gen. Pl. 2: 381. 1891. TYPE: Eastern Costa Rica, *Kuntze s.n.* (NY).

S. *roseus* Donnell Smith, Bot. Gaz. (Crawfordsville) 23: 249. 1897. TYPE: Costa Rica, confluence of the rivers Sarapiquí and Puerto Viejo, *Biolley 6922* (US, lectotype).

Centropogon radicans (Kuntze) McVaugh, Ann. Missouri Bot. Gard. 27: 353. 1940.

Sprawling, ascendant, somewhat suffrutescent *herbs*; stems to 1 m long and minutely puberulent, glabrate below. Principal *leaves* with blades ovate, mostly (4–)6–11.8 cm long, 2.5–4(–7.5) cm wide, usually 1.5–2 times as long as wide, apically acute to abruptly short-acuminate, basally rounded or somewhat tapering, marginally sharply and irregularly 1–2 times serrate with 2–4 larger teeth per cm, each of these with 1–4 smaller teeth, minutely puberulent on the veins beneath and to a lesser extent on the principal veins above, shiny and glistening green above and beneath; petioles 1.2–3 cm long. *Flowers* solitary in the axils of the upper leaves, 5–6.5 cm long; pedicels ascending, later widely spreading, puberulent, 4.5–9.5 cm long (in fruit), bearing 2 filiform basal bracteoles 1–2.5(–4)

FIGURE 2. *Centropogon coccineus* (Hook.) Regel.—A. Habit (×7/10).—B. Filament tube, anther tube, and exserted style (×3⅗). [After *Wilbur et al. 15597* (DUKE).]

mm long; hypanthium in anthesis turbinate to campanulate, puberulent, basally acute; calyx lobes linear-attenuate, puberulent, entire to indistinctly toothed, (4–)7–9(–12) mm long, erect or apically slightly spreading, light green; corolla bright red or scarlet, the lobes sometimes paler, roseate to pinkish externally,

white internally, externally puberulent or minutely spiculate, internally glabrous, the tube (3.6–)4–4.8 cm long, slightly arching, narrowest just above base where 3–4 mm in diameter, gradually enlarging above to 7–10(–13) mm in diameter and somewhat constricted again towards the apex, the lobes acute with the 2 upper lobes elliptic to oblong, 4.5–9 mm long, the 2 lateral lobes asymmetrically triangular, 5–7 mm long, the ventral lobe 6–10 mm long; filament tube glabrous, white, (35–)40–43 mm long, not exserted from the corolla tube, the anthers 6–7.5 mm long, the 2 shorter anthers apically and bristly white-tufted with dense trichomes 0.5–1 mm long, the other 3 anthers sparingly to moderately pilose apically with trichomes 0.5–1.5 mm long. *Berries* globose to broadly ellipsoid, mostly 1.5–2.5 cm long, 1.2–2.0 cm in diameter, white; seeds light brown, lenticular, nearly orbicular, foveate-reticulate, 0.4–0.5 mm in diameter.

This species is known from Costa Rica, Panama, and Colombia, usually at elevations of 1,000 m or less. Specimens from Costa Rica seemingly have lobes much paler in color than those from Panama.

BOCAS DEL TORO: Changuinola Valley, *Dunlop 222* (US), *341* (F, US). Changuinola to 5 mi S at junction of Ríos Changuinola and Terebé, 100–200 ft, *Lewis et al. 919* (DUKE, MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1946* (MO), *2132* (DUKE, MO). CANAL ZONE: Gatún, *Wagner 269* (M). COCLÉ: El Valle, *Aguilar 1* (MO, PMA). Vic. of El Valle, 800–1000 m, *Allen 212* (F, GH, MO). Vic. of El Valle, 600–1000 m, *Allen 1214* (GH, MO, NY). N of El Valle, *Allen 3688* (F, MICH, MO). El Valle de Antón, 900 m, *Alston 8722* (US). Vic. of El Valle, *Bartlett & Lasser 16704* (MO). El Valle, *Blum et al. 2385* (FSU, MO, SCZ, US). Las Delicias, *Carleton 222* (US). 1 km from top of Cerro Pilón, *Correa 44* (MO, PMA, SCZ). 2 mi above El Valle, *Croat 13304* (DUKE, MO). La Mesa above El Valle, 810 m, *Croat 25292* (MO). Forest behind Club Campestre, ca. 700 m, *Duke 13268(3)* (MO, REED). Hills above El Valle, ca. 1000 m, *Gentry 6870* (DUKE, F). La Mesa, 5 mi N of El Valle, 2500 ft, *Godfrey & Tyson 2455* (FSU). El Valle de Antón, *Gracia 46* (PMA). El Valle de Antón, along Río Indio trail, 500–700 m, *Hunter & Allen 310* (F, GH, MO). El Valle de Antón, La Mesa, ca. 1000 m, *Kennedy 3040* (DUKE, MO). Cerro Pilón, *Lallathin 5038* (MO, PMA). Hills NE of El Valle de Antón, 2000 ft, *Lewis et al. 1695A* (DUKE, MO). El Valle de Antón, *Lewis et al. 2544* (DUKE, MO). La Mesa above El Valle, 900 m, *Liesner 746* (DUKE). 5 mi N of El Valle de Antón, ca. 1000 m, *Luteyn 1171* (DUKE, F, MICH). 2.8 mi NW of El Valle de Antón, 3100 ft, *Luteyn 4060* (DUKE, LL). El Valle de Antón, 1840 ft, *Maurice 770* (US). El Valle de Antón, *Mendez 132* (US). La Mesa, 650–710 m, *Mori & Kallunki 1902* (MO). Cerro Pilón, 2000 ft, *Porter et al. 4454* (DUKE). El Valle, 500–700 m, *Seibert 424* (MO, US). Road from El Valle to La Mesa, 2400–2600 ft, *Spellman 582* (MO). Above El Valle, *Stimson 5020* (DUKE, SCZ). Above El Valle on road to La Mesa, 2500 ft, *Tyson 6936* (PMA). La Mesa, 5 mi N of El Valle, *Tyson & Godfrey 2455* (SCZ). La Mesa above El Valle de Antón, 1000 m, *Weaver & Foster 1661* (DUKE, PMA). Inside the crater of El Valle de Antón, La Mesa, ca. 1000 m, *Wilbur et al. 11109* (DUKE, F, MO, NY, PMA, US), *11124* (DUKE, F, MO, PMA). Trail to La Mesa ca. 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11676* (DUKE, MO, PMA, US). Narrow valley behind Hotel Pan Americana, *Wilbur & Luteyn 11715* (DUKE, MO, US). Cerro Pajita in crater of El Valle de Antón, *Wilbur et al. 15597* (DUKE, F, MICH, MO). La Mesa, in the crater of El Valle, forest, ca. 850 m, *Wilbur et al. 15639* (DUKE, MICH). Bismark, *Williams 260* (NY). N rim of El Valle de Antón, near Cerro Turega, 650–700 m, *Woodson & Schery 166* (MO). COLÓN: 4 km NW of Salamanca, 13 km NE of Buenos Aires, *Nee 9068* (DUKE). PANAMÁ: Río Chagres, 1 mi above Madden Lake, *Duke 4466* (GH, MICH, MO). Headwaters of Río Corso, ca. 500 m, *Duke 11909* (MO). Cerro Jefe, *Dwyer & Gauger 7331* (MO). Cerro Jefe, 2900 ft, *Dwyer & Gentry 9515* (DUKE, MO). Cerro Campana, *Ebinger 335* (F, MO, US). Cerro Campana above Su Lin Motel, *Gentry 1825* (MO, SCZ). Altos del Río Pacora, 2500 ft, *Lewis et al. 2292* (DUKE, MO). Tributary of Río Chagres, 5 mi SW of Cerro Brewster, ca. 1000 ft, *Lewis et al. 3450* (DUKE, MO). Cerro Campana, 8.6 mi SW of Capira, 700–800 m, *Luteyn 1042* (DUKE, MICH). Beyond La Eneida, ca. 1000 m, *Luteyn & Foster 1116* (MICH, MO).

Junction of Ríos Pacora and Corso to headwaters of Río Corso, *Oliver 2358* (MO). Above Alhajuela, *Pittier 3508* (US). Slopes of Cerro Jefe beyond Cerro Azul, *Wilbur & Weaver 11347* (DUKE, MO). VERAGUAS: 8.8 km beyond Escuela Agrícola NW of Santa Fé, *Cochrane 6215* (MO). Río Primero Brazo, 2.5 km beyond Agriculture School near Santa Fé, 700–750 m, *Croat 25485* (MO). 3.9–5 mi N of Santa Fé, 500–1000 m, *Gentry 3002* (MO). Above Río Primero Brazo 5 mi NW of Santa Fé, *Liesner 1004* (MO). Forest above Escuela Agrícola Alto de Piedra, just W of Santa Fé, 3200 ft, *Luteyn 4003* (DUKE, MICH). NE slopes of Cerro Delgadito just NW of Cerro Tute, S of Santa Fé, ca. 1000 m, *Luteyn 4017* (DUKE). N of Santa Fé, ca. 2 km N of Escuela Agrícola, *Mori & Kallunki 2611* (MO). NW of Santa Fé, 2.7 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 6213* (DUKE, MO). N of agricultural camp and ca. 2 km N of Santa Fé, *Wilbur & Luteyn 19111* (DUKE), *19130* (CAS, DUKE, F, GH, LL, MICH, MO, NY, US, WIS).

2. **Centropogon congestus** Gleason, Bull. Torrey Bot. Club 52: 52. 1925. TYPE: Colombia, Dept. Caldas, Pereira, 1400–1500 m, *Pennell 10169* (NY).

C. diocleus F. E. Wimmer, Ann. Missouri Bot. Gard. 24: 209. 1937. TYPE: Panama, *Seibert 166* (W, holotype, not seen; GH, MO, NY, isotypes).
C. macrophyllus (G. Don) F. E. Wimmer var. *congestus* (Gleason) McVaugh, Ann. Missouri Bot. Gard. 27: 352. 1940.

Suffrutescent, relatively unbranched, erect *herbs* 1–2(–3?) m tall; stems glabrous or nearly so below the inflorescence. Median cauline *leaves* with blades elliptic to somewhat oblanceolate to obovate, (10–)15–30(–39) cm long, 6–12 cm wide, mostly 2.5–4 times as long as wide, drying thin and membranous, apically acute to acuminate, basally cuneate, marginally moderately to coarsely doubly serrate, glabrous above and moderately to densely spreading short-pubescent beneath at least along the principal veins and often through the 4th order with slender-based trichomes 0.1–0.2 mm long, otherwise glabrous; petiole (1.5–)2–6 cm long. *Inflorescences* 5–18(–25) cm long, 8–40-flowered in a usually dense, racemose cluster, terminal or rarely cauliflorous beneath the terminal cluster of leaves; peduncle moderately to densely spreading, short-pubescent, mostly (3–)6–15 cm long; bracts reduced, thin, petiolate, foliaceous, 1–6 cm long, 0.8–2.0 cm wide. *Flowers* 3.5–4.8 cm long; pedicels mostly 2–6 cm long at maturity, moderately to densely spreading short-pubescent, the trichomes slender, straight and 0.1–0.3 mm long, the bracteoles linear, mostly 4–6 mm long, borne (0.3–)0.8–1.6 cm above the pedicel base; hypanthium moderately to densely spreading-short-pubescent, hemispheric, rounded to somewhat truncate basally, 4–6 mm high; calyx lobes linear to narrowly triangular, erect, 0.9–1.5(–1.7) cm long, ca. 2 mm wide at the base, acute, entire to minutely and irregularly toothed, moderately short-pubescent; corolla bright rose-purple or reddish pink, moderately to densely spreading short-pubescent externally, the slender trichomes 0.1–0.2 mm long and only slightly if at all wider at the base than at the midpoint, glabrous internally, the tube 2.8–3.4(–3.8) cm long, moderately to strikingly curved in the upper third, 4–6 mm in diameter below the bend and expanding above to 6–9(–13) mm in diameter at the throat, the 2 upper lobes erect to slightly falcate, 7–9 mm long, acute, the 2 lateral lobes triangular, acute, with a falcate tip, 5–7 mm long, the lowermost lobe triangular, 5–7 mm long, erect, acute; filament tube 30–38 mm long, glabrous, sometimes spreading-short-pubescent apically, pale reddish, slightly exserted, the anther tube blackish, 4–6 mm long, glabrous to sparingly short-pilose on the connectives, the trichomes 0.5–0.8 mm long, the shorter, lower

anthers terminated by a stiff concrescent, triangular scale 2–3 mm long. *Berries* relatively thin-walled, subglobose and somewhat angular, 0.8–1.4 mm in diameter; seeds plumply lenticular, foveate-reticulate, dark brownish, ca. 0.5 mm long.

In southern Central America *Centropogon congestus* is known only from the mountains of Chiriquí and Bocas del Toro and from central Costa Rica. As pointed out by McVaugh (1940) these populations are apparently indistinguishable from the Colombian *C. congestus*. McVaugh felt that *C. congestus* is at best varietally differentiated from the Peruvian *C. macrophyllus* (G. Don) F. E. Wimmer. Wimmer's and Gleason's concepts were obviously more narrowly defined than were those of McVaugh. Wimmer recognized both *C. macrophyllus* and *C. congestus* as species belonging to grex *Amplifolii* A. Zahlbr. of subsect. *Corymboides* F. E. Wimmer, a group characterized by usually compact, subumbellate or corymbose racemes; these differ from one another in that *C. macrophyllus* has glabrous or nearly glabrous leaves, corollas, and hypanthia, while *C. congestus* is distinctly hirsutulous or puberulous. Wimmer also maintained *C. diocleus* as a distinct species placing it in subsect. *Axillares* Gleason. *Centropogon diocleus* has a compact terminal corymbiform raceme like members of subsect. *Corymboides* and is unlike subsect. *Axillares* which is characterized by solitary flowers borne in the axils of unreduced or little reduced vegetative leaves. Wimmer's statement that *C. diocleus* has solitary flowers in the axils of the upper leaves is not in accord with the isotypes examined, including the isotype at MO which Wimmer implied was seen by him. Specimens of *C. congestus* seen from Colombia vary most noticeably in degree of pubescence and the length of the trichomes, but many Colombian plants seem indistinguishable from specimens from southern Central America. Study of more and better collections is needed before the specific distinctness or interrelationships of such taxa as *C. macrophyllus*, *C. gesneraeformis* Drake, and *C. gesneroides* Gleason can be properly determined.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4936* (MO). CHIRIQUÍ: Vic. of "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1393* (GH, MO, NY). Quebrada Velo, vic. of Finca Lérida, 5000 ft, *Allen 4673* (MO). Cerro Punta, ca. 7000 ft, *Blasdell 368* (FSU). Vic. of Las Nubes, 2.7 mi NW of Río Chiriquí Viejo W of Cerro Punta, 2200 m, *Croat 22406* (MO). Bajo Chorro, *Davidson 209* (F, GH, MO). Collin's Finca, *Ebinger 668* (US). Horqueta, 6500 ft, *von Hagen 2007* (NY). Collin's Finca, *Hayden 165* (MO). Las Nubes, NW of Cerro Punta, 1900–2100 m, *Luteyn 3808* (DUKE). Bajo Chorro Trail from Paso de Respinga to Fila de Respinga, 2360–2500 m, *Luteyn 3815* (DUKE). Vic. of Cerro Punta, 6800 ft, *Ridgway & Solis 2392* (MO). Valley of the Río Chiriquí Viejo, *Seibert 166* (GH, MO, NY). Bambito, 1 mi SW of Cerro Punta, 5600 ft, *Tyson 5650* (DUKE, FSU, MO). Las Nubes region, ca. 3–5.5 km NW of Cerro Punta, 2000–2410 m, *Utley et al. 239* (DUKE). Ca. 2 mi NE of Cerro Punta, 7000 ft, *Wilbur & Teeri 13098* (DUKE). Ca. 5 km NW of the town of Cerro Punta, 2000–2300 m, *Wilbur et al. 15200* (CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Ca. 3 km W of Cerro Punta, 2000 m, *Wilbur et al. 15266* (DUKE, MICH, MO). Upper Río Chiriquí Viejo, ca. 2 km NE of Guadelupe, *Wilbur et al. 15332* (DUKE, F, LL, MICH, MO). N side of Río Chiriquí Viejo, ca. 3.5 km from Cerro Punta, *Wilbur et al. 15351* (DUKE). Vic. of Las Nubes, W of peak of Cerro Punta, 6000–7000 ft, *Wilbur & Almeda 17067* (DUKE, F, LL, MICH, MO, PMA, US). Between Cerro Punta and Boquete, 8200 ft, *Wilbur & Luteyn 17250* (DUKE). 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn 19236* (DUKE). W of Las Nubes, ca. 5 km NW of Cerro Punta towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19350* (DUKE, MICH), *19395* (DUKE). Quebrado Velo, 1800 m, *Woodson & Schery 273* (GH, MO). Vic. of Bajo Chorro, 1900 m, *Woodson & Schery 614* (MO). Bajo Mano, mouth of Quebrado Chiquero along Río Caldera, 1500–2000 m, *Woodson et al. 1021* (GH, MO, NY).

3. **Centropogon cornutus** (L.) Druce, Bot. Exch. Club Brit. Isles 3: 416. 1914.

Lobelia cornuta L., Sp. Pl. 930. 1753. TYPE LOCALITY: "Cayenna."
L. surinamensis L., Sp. Pl., ed. 2. 1320. 1763. TYPE LOCALITY: Surinam.
L. obscura L., Pl. Surin. 14. 1775. TYPE LOCALITY: Surinam.
L. laevigata L. f., Suppl. Pl. 392. 1781. TYPE: Surinam, *Dalberg s.n.* (not seen).
L. andropogon Cav., Anal. Hist. Nat. 2. 106. 1800. TYPE: Ecuador, *Née s.n.* (not seen).
L. spectabilis H. B. K., Nov. Gen. Sp. Pl. 3: 306. 1819. TYPE LOCALITY: Venezuela.
L. purpurea Vell., Fl. Flum. Icon 8: *pl. 156.* 1827. TYPE LOCALITY: Brazil.
Siphocampylus macranthus Pohl, Pl. Bras. Icon. 2: 105, *pl. 168.* 1831. TYPE LOCALITY: Brazil.
S. spectabilis (H.B.K.) G. Don, Gen. Syst. 3: 702. 1834.
S. surinamensis (L.) G. Don, Gen. Syst. 3: 702. 1834.
S. andropogon (Cav.) G. Don, Gen. Syst. 3: 703. 1834.
Centropogon surinamensis (L.) Presl, Prodr. Monogr. Lobel. 48. 1836.
C. laevigatus (L.f.) A. DC., Prodr. 7: 344. 1829.
C. andropogon (Cav.) A. DC., Prodr. 7: 345. 1839.
Lobelia sphaerocarpa Juss. ex. A. DC., Prodr. 7: 345. 1839, pro syn.
Centropogon fastuosum H. Jacq., Ann. Fl. Pom. II. 3: 118. 1845.

Suffrutescent *herbs* 1–3 m tall, often somewhat scandent; stems simple or branched, hollow, glabrous in the lower portions and short, spreading, stiff-pubescent above. Median cauline *leaves* with blades oblong to ovate-oblong, elliptic-oblong to elliptic, 10–15(–25) cm long, usually 2–3 times as long as wide, apically acute or acuminate, basally rounded to cuneate, marginally subentire to obscurely denticulate or shallowly crenate-denticulate with 3–8 sharp teeth per cm, glabrous above and glabrous to minutely scaberulous on the veins beneath; petiole 0.5–2 cm long. *Flowers* solitary in the axils of the upper leaves, 6–8 cm long; pedicels erect, sparsely to densely puberulent, (3.5–)4.5–7(–9.5) cm long, the bracteoles paired, ciliate, linear 4–10(–15) mm long, borne at or near the pedicel base; hypanthium glabrous to bristly-pubescent; calyx lobes narrowly lanceolate to linear or linear-subulate, denticulate, often marginally short bristly-pubescent, 8.5–20 mm long, usually wide-spreading at maturity; corolla red or pink, the lobes often white or occasionally the corolla completely white, the tube 3.5–4.5 cm long, moderately to strongly curved throughout its length, narrowest basally and gradually widening upward, glabrous, sparingly hirsute, pilose, or sparingly spreading short-pubescent along the principal veins externally, glabrous internally, the lobes spreading, falcate, deltoid, the 2 upper lobes 7–9 mm long, the 3 lower lobes slightly shorter, all lobes marginally bearing stiff whitish hairs 0.5–1.2 mm long; filament tube 46–60 mm long, white or white and distally pink, glabrous below, distally sparsely to moderately pilose with the trichomes 1.5–3(–5) mm long, basally distinct and united to the corolla tube, the anther tube 7.5–9.5 mm long, densely hirsute especially along the connectives and at the base and apex, the trichomes mostly 1.5–2.5 mm long, the terminal pubescence of the 2 shorter anthers fused into a triangular, hardened scale ca. 3 mm long. *Berries* scarcely inflated, a little broader than high, 10–17 mm in diameter; seeds flattened with rounded edges, more or less circular in outline, 0.6–1.8 mm in diameter, shallowly foveate-reticulate.

This species has been reported from Mexico (Oaxaca), Panama, the Lesser Antilles, and throughout northern South America—especially the lowlands—south to Bolivia and southern Brazil.

BOCAS DEL TORO: Fish Creek Hills, vic. of Chiriquí, *von Wedel 2408* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Aviles 81b* (F, MO). Gatún Station on Panama Railroad, *Hayes 77* (GH). Empire to Mandinga, *Piper 5441* (US). Near Culebra, 50–290 m, *Pittier 2221* (C, F, GH, NY, US). Barro Colorado Island, *Shattuck 424* (F, MO). Las Cascadas Plantation, near Summit, *Standley 29575, 25714, 25758* (all US). Vic. of Fort Sherman, *Standley 31056* (US). COLÓN: Roadside W of Portobelo, *D'Arcy 4070* (MO). Between Río Guanche and Río Iguanita, 20 m, *Dressler 4898b* (DUKE). Ca. 1 km S of Portobelo, *Gentry & Née 8757* (DUKE). Santa Rita Hills, *Smith & Smith 3415* (F, US). DARIÉN: Vic. of Caná, 1750 ft, *Stern et al. 463* (GH, MO, US). Old town of Caná, 1750 ft, *Stern et al. 486* (MO). PANAMÁ: Cerro Trinidad, 800–1000 m, *Allen 3769* (GH, MICH, MO). Near settlement of Aguacate, ca. 1 mi N of Cerro Trinidad, 350 m, *Foster 2147* (DUKE, PMA).

4. **Centropogon darienensis** Wilbur.[13] TYPE: Panama, *Gentry & Mori 14064* (MO, holotype; DUKE, isotype).

Perennial *herbs* 40–50 cm tall; stems fistulose, 2–5 mm in diameter, glabrate throughout or sparingly puberulous above. Principal cauline *leaves* with blades drying thinly membranous, usually elliptic to vaguely oblong-elliptic, apically acute to acuminate, basally acutely tapering, 12–22 cm long, 5.0–7.8 cm wide, marginally indistinctly serrulate to denticulate, the teeth projecting 0.1–0.2 mm from the blade and spaced 3–7(–9) mm apart, glabrous above and beneath or sparingly strigillose on the elevated veins beneath; petioles 1–2.5 cm long, glabrous. *Inflorescences* terminal, corymbiform or umbellate racemes 5–8 cm long apparently with few (4–8) flowers. *Flowers* 4.5–5.5 cm long; peduncle inconspicuously hirsutulous; bracts several, subsessile, 2–3 cm long; pedicels hirsutulous, 5–10 mm long, the trichomes 0.1–0.2 mm long; bractlets paired, 0.8–1.0 mm long 2–5 mm from the pedicel base. *Flowers* with the hypanthium densely but microscopically granular-spiculate, campanulate, 2.5–3.5 mm high, 4–6 mm in diameter at anthesis; calyx lobes linear, inconspicuously ciliate with trichomes less than 0.1 mm long, entire to inconspicuously toothed, 4–6 mm long, 1.0–1.5 mm wide, erect; corolla tube red, ca. 3.5 cm long, strongly bent just above the middle to form an angle of 80°–90°, in the basal half 3–4 mm in diameter, strongly flaring above to 8–11 mm in diameter, densely though inconspicuously beset externally with short, conical protuberances; corolla lobes falcate or narrowly triangular, 5–7 mm long, acute to acuminate, red and similar to the tubes in color; filament tube ca. 4.5 cm long, slightly exserted, glabrous, the anther tube 5–9 mm long, externally glabrous or sparsely pubescent, the lowermost anthers with a triangular white scale-appendage composed of concrescent trichomes ca. 3 mm long and internal to a fringe of straight, white, trichomes 1.0–1.2 mm long. *Berries* unknown.

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[13] *Centropogon darienensis* Wilbur, sp. nov. Herbae erectae glabrae 40–50 cm altae. Lamina foliorum elliptica membranacea, apice acuta vel acuminata, basi acuti, 12–22 cm longa et 5.0–7.8 cm lata, margine serrulata vel denticulata, denticula 0.1–0.2 mm longa et ca. 1–3 per cm; petioli glabri, 1–2.5 cm longi. Flores 4–8 in racemo brevi corymbosa terminali, 4.5–5.5 cm longi; pedunculi hirsutuli; bractae 2–3 cm longae; pedicelli 5–10 mm longi, hirsutuli; bracteolae 0.8–1.0 mm longae. Hypanthia squamulosa-hirtella, campanulata, 2.5–3.5 mm alta et 4–6 mm diametro; lobi calycis lineari, ciliati, integri vel denticulati, erecti, 4–6 mm longi et 1–1.5 mm lati. Corollae rubrae, tubi ca. 3.5 cm longi, curvati; lobi falcati, 5–7 mm longi, acuti vel acuminati. Filamenta 4–5 cm longi, exserti, glabri; anthearum tubus 5–9 mm longus cornutus.

This species is known only from the type collection.

DARIÉN: Cerro Tacarcuna, 1550–1650 m, *Gentry & Mori 14064* (DUKE, MO).

5. **Centropogon ferrugineus** (L.f.) Gleason, Bull. Torrey Bot. Club 52: 11. 1925.

Lobelia ferruginea L.f., Suppl. Pl. 394. 1781. TYPE LOCALITY: Bogota, Colombia.
L. barbata Cav., Icon. Descr. Pl. 6: 12, *pl. 519*. 1801. TYPE: "In regno Peruviano prope Guamatanga et Obragillo," *Nee* (not seen).
Siphocampylus ferrugineus (L.f.) G. Don, Gen. Syst. 3: 701. 1834.
S. barbatus (Cav.) G. Don, Gen. Syst. 3: 701. 1834.
Centropogon barbatus (Cav.) Planch., Fl. Serres 6: 16. 1850–1851.
C. costaricanus Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren Kjøbenhavn 1857: 156. 1857. TYPE: Costa Rica, Volcán Irazú, *Oersted 9240* (C, holotype and isotype).
Siphocampylus regelii Vatke, Linnaea 38: 732. 1874. TYPE: Costa Rica, Irazú, *Wendland 679* (B, not seen).
S. regelii var. *β umbrosus* Vatke, Linnaea 38: 733. 1874. SYNTYPES: Guatemala, Costa Rica, or "Veragua," *Warscewicz 2, 4, 6* (B, none seen).
Centropogon affinis Mart. & Gal. var. *costaricanus* (Planch. & Oerst.) Zahlbr., Ann. Naturhist. Mus. Wien 6: 437. 1891.
C. affinis var. *venezuelanus* F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 242. 1924. TYPE LOCALITY: Venezuela.
C. poasensis Gleason, Torreya 25: 92. 1925. TYPE: Costa Rica, Alajuela Prov., Volcán Poás, *Donnell Smith 6626* (NY, holotype; GH, M, US, isotypes).
C. costaricanus var. *tomentellus* F. E. Wimmer, Ann. Naturhist. Mus. Wien 46: 240. 1933. TYPE: Costa Rica, Alajuela Prov., Volcán Poás, *Cufodontis 541a* (B, not seen).
C. costaricensis var. *cufodontidis* F. E. Wimmer, Ann. Naturhist. Mus. Wien 46: 240. 1933. TYPE: Costa Rica, Alajuela Prov., Volcán Poás, *Cufodontis 541b* (B, not seen).
C. ferrugineus var. *venezuelanus* (F. E. Wimmer) McVaugh, Ann. Missouri Bot. Gard. 27: 351. 1940.
C. ferrugineus var. *costaricanus* (Planch. & Oerst.) McVaugh, Ann. Missouri Bot. Gard. 27: 352. 1940.
C. ferrugineus var. *tomentellus* (F. E. Wimmer) McVaugh, Fl. N. Amer. 32A: 126. 1942.

Suffrutescent *herbs*; stems hollow, arching or sprawling, 1–3(–4) m tall, glabrous below and sparsely to densely dendritic-pubescent above. Median cauline *leaves* with blades oblong to elliptic, 5–15(–21) cm long, 2–5(–8) cm wide, apically acute to abruptly acuminate or less commonly rounded, basally rounded to gradually tapering, marginally sharply denticulate with 6–10, 0.2–0.5 mm long teeth per cm, glabrous or nearly so above except on the principal veins, beneath sparingly to densely dendritic-pubescent; petiole (–0.5)1–3(–4) cm long. *Flowers* solitary in the axils of the upper leaves, ca. 5 cm long; pedicels glabrate to densely dendritic-pubescent, 4–9.5 cm long; bracteoles 2, linear-filiform, 1–2 mm long near the pedicel base; hypanthium hemispheric, 3–5 mm high, sparingly to densely pubescent with dendritic trichomes; calyx lobes narrowly triangular, entire to moderately denticulate, acute, sparingly dendritic-pubescent, (1.6–)2–4(–6) mm long, more or less erect, green to dark purplish; corolla dull reddish to orange externally, yellowish within, moderately to densely dendritic-pubescent externally and glabrous within, the tube (1.5)2–2.8 cm long, slightly curved, the contracted portion just above the somewhat swollen base ca. 7–10 mm long, 2–3(–4) mm in diameter, then expanding above to 7–8(–10) mm in diameter, the lobes falcate, acuminate, the 2 upper lobes 8–12(–15) mm long, the

lower 3 lobes 5–9 mm long; filament tube 3–3.7 cm long, conspicuously exserted, softly pubescent throughout with unbranched hyaline trichomes, basally distinct and adherent to the contracted basal section of the corolla tube; anther tube 7–8 mm long, the 2 shorter anthers conspicuously white-tufted apically, the anthers otherwise glabrous or with a few elongate trichomes (1–)2–3 mm long on the connectives. *Berries* leathery, surmounted by a 1–3 mm high rim; seeds short-ellipsoid, flattened, foveate-reticulate.

This species occurs in mountains from Guatemala south through the Andes into Peru.

As suggested by the synonymy listed above, *Centropogon ferrugineus* sensu lato is an extremely variable species. Wimmer (1943) recognized about 75 species in this largely Andean group (Grex *Stellato-tomentosi* Gleason ex. F. W. Wimmer). He recognized *C. ferrugineus* as occurring only in South America and treated all Central American members with branched trichomes as *C. costaricanus*. This species in his opinion was divisible into three varieties based on type of pubescence, leaf shape, and calyx-lobe length. McVaugh (1940, 1943) also recognized only one species with dendritic trichomes in Central America but felt that it is conspecific with the northwestern South American *C. ferrugineus*. McVaugh's concept of *C. ferrugineus* is considerably broader than that of Wimmer, and like Wimmer, McVaugh recognized three varieties with dendritic trichomes as occurring in Central America. McVaugh separated the infraspecific taxa as follows:

a. Pubescence often sparse, light yellow or yellow brown to gray brown.
  b. Pubescence light yellow or yellow brown; leaves tapering from about the middle to the apex and not abruptly pointed ..... *C. ferrugineus* var. *venezuelanus*
  bb. Pubescence light gray brown; leaves usually abruptly narrowed into a short-acuminate point ..... *C. ferrugineus* var. *costaricanus*
aa. Pubescence usually dense and fluffy, at least in the inflorescence, consisting of rich dark brown hairs ..... *C. ferrugineus* var. *tomentellus*

These morphological variants may not be geographically segregated or useful taxa, but careful field observations would help resolve this problem. McVaugh (1943) indicated that both var. *venezuelanus* and var. *costaricanus* occur in western Panama (Chiriquí) and that var. *tomentellus* is restricted to central Costa Rica (Poás).

BOCAS DEL TORO: N slopes of Cerro Horqueta, Robalo Trail, 6000–7000 ft, *Allen 4947* (MICH, MO). CHIRIQUÍ: Potrero Muleto, Volcán de Chiriquí, 10400 ft, *Davidson 1015* (F, GH, MO, US). Bajo Chorro Trail, 2360–2500 m, *Luteyn 3828* (DUKE, MO). Cerro Pando at the Costa Rican-Panamanian border, 2000–2482 m, *Mori & Bolten 7325* (DUKE, MO). 2.5 km SE of Cerro Punta, *Mori & Kallunki 5650* (DUKE, MO). Trail through the Paseo de Respinga, 7500 ft, *Wilbur et al. 13167* (CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, WIS, US). Trail through Paseo de Respinga, 8000 ft, *Wilbur & Teeri 13194* (DUKE, MO). Trail to Boquete from Cerro Punta, 2100–2400 m, *Wilbur et al. 15122* (DUKE). Trail from Bajo Grande along Quebrado Grande to top of Paso de Respinga, 2100–2400 m, *Wilbur et al. 15134* (DUKE, F, MICH, MO, US). Cerro Punta, 8700 ft, *Wilbur et al. 17117* (DUKE, MO), *17126* (DUKE), *17139* (DUKE, MO). Portrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 447* (GH, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 845* (AA, MO, NY).

6. **Centropogon floricomus** McVaugh, J. Wash. Acad. Sci. 39: 160. 1949. TYPE: Panama, *Allen 4911* (MICH, holotype; F, GH, MO, US, isotypes).

Herbs 0.4–0.6 (–1.0) m tall; stems erect to sprawling, hollow, glabrous below and sparsely appressed-puberulent above. Median cauline *leaves* with blades lance-ovate, (4–)6–10(–13) cm long, 1.5–3(–4.5) cm wide, ca. 2.3–2.8 times as long as wide, apically tapering into a narrow, caudate apex often 2–3 cm long, basally rounded to subcordate and occasionally somewhat asymmetric, marginally finely and shallowly serrate to denticulate with 5–6 callose-tipped teeth per cm, glabrous above except for the puberulence on the impressed, principal veins and puberulent beneath on the elevated, principal veins; petiole puberulent, (0.8–)1.0–2.5 cm long. *Flowers* solitary in the axils of the upper leaves, 6.5–7 cm long on sparsely puberulent, weakly spreading and flexuous pedicels 6–8 cm long; bracteoles 2, minutely puberulent, linear, 1–3 mm long, borne 3–5 mm above the base; hypanthium in anthesis campanulate to turbinate, basally acute, puberulent, 8–9 mm long, 6 mm in diameter with a free rim ca. 1 mm high; calyx lobes erect but arching outward apically, acute, narrowly triangular to linear, 4–5 mm long, puberulent, entire or with a pair of glandular basal teeth; corolla bright pink, tipped with white lobes, the tube 4.0–4.6 cm long, externally minutely puberulent, internally glabrous, straight or slightly bent at the base, the basal portion constricted, cylindrical, 10–15 mm long, 2–4 mm in diameter, expanding above into a narrowly funnelform throat 6–9 mm in diameter, the lobes linear, the upper 2 lobes 16–18 mm long, erect, acute and often with stiff hyaline hairs near the tip, the 2 lateral lobes 12–13 mm long, reflexed, the lowermost lobe 10–12 mm long, curving downward; filament tube 50–55 mm long, longer than the corolla tube but not extending beyond the corolla lobes, glabrous, the lower third basally distinct and there fused with the corolla tube; anther tube 7.5–8 mm long, glabrous except for the dense tuft of stiff hairs 1–2 mm long at the tip of the 2 shortest anthers. *Berries* leathery, pendent, strongly angled, somewhat inflated; seeds ovoid-lenticular, reticulate-pitted.

This species is known only from the wet mountain slopes of Bocas del Toro and Chiriquí in the vicinity of Cerro Horqueta on the eastern (Boquete) side of Volcán Barú and near Cerro Punta on the western side of Barú at an elevation of 1,800–2,100 m. Its closest affinities are with *C. gutierrezii* which occurs in the Costa Rican Cordillera Central and on Cerro Pando of the Costa Rica-Panama border and with Costa Rican *C. talamancensis* Wilbur. It differs from both these species by numerous features of which its shorter calyx lobes are diagnostic.

BOCAS DEL TORO: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft, *Allen 4911* (F, GH, MICH, MO, US). CHIRIQUÍ: Above Las Nubes, NW of Cerro Punta, 1900–2100 m, *Luteyn 3798* (DUKE, MICH, MO). Vic. of Las Nubes, 2.7 mi NW of Río Chiriquí Viejo, 2200 m, *Liesner 292* (DUKE). Trail beyond Las Nubes to about midway between Cerro Picacho and Cerro Punta, *Luteyn & Wilbur 4625* (DUKE), *4637* (DUKE, MICH, MO, NY). Las Nubes region, 3–5.5 km NW of Cerro Punta and 2 km NW of Las Mirandes, 2000–2410 m, *Utley et al. 250* (DUKE, F, MICH, MO, PMA, US). Vic. of Las Nubes, ca. 6 km NW of town of Cerro Punta, 6000–7200 ft, *Wilbur et al. 17082* (DUKE, MO). Vic. of Las Nubes, 7200 ft, *Wilbur et al. 17161* (DUKE, GH, LL, NY). Ravine W of Las Nubes towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19374* (DUKE, F, GH, MICH, MO, US).

7. **Centropogon granulosus** Presl, Prodr. Mongr. Lobel. 49. 1836. TYPE LOCALITY: Peru.

C. cuspidatus A. DC., Prodr. 7: 346. 1839. TYPE: Peru, *Dombey* (P, not seen).
C. densiflorus Benth., Pl. Hartw. 138. 1844. TYPE: not seen.
C. nutans Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn. 1857: 156. 1857. TYPE: Costa Rica, Turrialba, *Oersted* (not seen).
Siphocampylos corymbiflorus K. Koch, Wochenschr. Verenines Beförd. Gartenbaues Königl. Preuss. Staaten 7: 60. 1864. TYPE: not seen.
Centropogon warscewiczii Vatke, Linnaea 38: 716. 1874. SYNTYPES: Costa Rica and "Veraqua," Panama, *Warscewicz 3, 5* (B, neither seen).
C. tortilis F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 22: 217. 1926. TYPE: Costa Rica, *Pittier 16033* (W, holotype, not seen; CR, GH, isotypes).
C. erastus F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 8. 1935. TYPE: Costa Rica, Palma, *Brade 2395* (B, holotype, not seen).
C. augostanus F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 9. 1935. TYPE: "Mexico [Costa Rica], Prov. Cartago," *Polakowsky 431* (B, holotype, not seen).

Arching or sprawling, scandent, suffrutescent *herbs*; stems glabrous, granular-scabrous to inconspicuously short-pubescent above, 1–2.5 m long, to 1.5 cm in diameter, hollow at maturity. Median cauline *leaves* with blades usually broadly elliptic to oblong or ovate, (8–)10–20(–32) cm long, 5–10(–13) cm wide, mostly 2.5–3 times as long as wide, apically acute or short-acuminate, basally rounded, subcordate or cuneate, marginally indistinctly serrulate or sinuate-crenate with mostly 1–4, pale yellowish callose teeth per cm, glabrous above, beneath glabrous to inconspicuously scaberulent, especially on the principal veins where often granular, spiculate, or inconspicuously short-pubescent; petioles 0.5–1.5(–2.5) cm long. *Inflorescences* pendent, at first compact, umbellate, elongating into irregular racemes 6–15(–30) cm long, loosely to densely, 3–25(–100)-flowered with the flowers borne singly in the axils of foliaceous bracts; bracts mostly 1–2.5 cm long; peduncle usually conspicuous, 6–15(–20) cm long; pedicels sparingly to copiously granular-pustulate, spreading to ascendent, mostly 2–4(–6) cm long, ca. 1 mm in diameter; bracteoles subbasal, linear, 1–3(–6) mm long. *Flowers* 5–7 cm long; hypanthium nearly glabrous to densely granular-spiculate, rarely short-pubescent, at anthesis 6–9(–12) mm in diameter and 4–7 mm high, hemispheric; calyx lobes linear, inconspicuously bristly, short-pubescent, entire to inconspicuously and remotely denticulate, (4–)8–19 mm long; corolla tube red and orange, 2.8–4.0 cm long, proximally nearly straight, distally nearly straight to strongly arching or curved abaxially, basally 6–8 mm in diameter, contracting ca. 5 mm from the base to 2.5–4.5 mm in diameter, in the upper third abruptly flaring to (10–)12–15 mm, sparsely to densely beset externally with short, conical protuberances, these rarely completely lacking, glabrous within, the lobes deltoid, acuminate, the lateral lobes falcate, the 2 uppermost lobes reflexed, 8–12 mm long, orange yellow, the 3 lower lobes reddish, reddish orange, or yellowish, the lower and lateral lobes 4–8 mm long, rarely epapillate, mostly with short, conical protuberances; filament tube 4–5.5 cm long, exserted 4–8(–12) mm from the corolla tube, pale yellowish, distally sparingly to densely hirsute with spreading coarse hyaline trichomes 1–2 mm long, basally the filaments distinct from one another but united to the narrowed corolla tube, the anther tube 7–10 mm long, apically white-tufted, the trichomes of the 2 shorter and lowermost anthers

partially concrescent into a triangular scale 2.2–3.0 mm long and externally with a fringe of trichomes about half as long, the connectives sparsely to densely hirsute with hyaline trichomes mostly (1–)2–3 mm long. *Berries* broader than high, leathery, 9–15(–20) mm in diameter; seeds lenticular, nearly circular, shallowly foveate-reticulate, ca. 0.7 mm in diameter.

Centropogon granulosus is commonly encountered in wet montane habitats in Chiriquí Province, in Costa Rica, and also in South America from Colombia south into Peru. Wimmer (1943) recognized *C. nutans* and *C. granulosus*, although admitting that some Colombian collections seemed intermediate. He distinguished the two as follows: the North American *C. nutans* allegedly has calyx lobes 10–11 mm long and the South American *C. granulosus* has lobes 8 mm or less long. Wimmer also recognized three species (*C. tortilis*, *C. erastus* and *C. augostanus*) based to a considerable extent upon leaf shape. McVaugh's (1940) more inclusive concept of this complex seems more plausible and is followed here.

Another variable feature of this species is the abundance of short conical projections on the corolla. The corollas are usually moderately to densely covered with these granular protuberances but certain specimens lack them completely and others are only sparsely supplied with them. This tuberculate scabrosity may also be found on the hypanthia, pedicels, and stems. Wimmer recognized *C. granulosus* var. *rutilus* from Colombia and Ecuador for plants of the nontuberculate type. Apparently similar specimens occur in Costa Rica and Panama.

BOCAS DEL TORO: N slopes of Cerro Horqueta, Robalo Trail, 6000–7000 ft, *Allen 4923* (MICH, MO, NY). Chiriquicito-Caldera Trail, between Quebrada Higuerón and Gutierrez, *Kirkbride & Duke 743* (MO, REED). CHIRIQUÍ: Río Chiriquí Viejo, 1200 m, *Allen 985* (GH, MO). Vic. of "New Switzerland," central valley of Río Chiriquí Viejo, 1800–2000 m, *Allen 1420* (F, GH, MO, US). Vic. of Cerro Punta, 2000–2500 m, *Allen 3519* (GH, MICH, MO, NY). W slopes of Cerro Horqueta, Bajo Mono-Robalo Trail, 5000–7000 ft, *Allen 4792* (MO). Cerro Punta, ca. 7000 ft, *Blaisdell 346* (FSU), *368* (MO). Cerro Punta, 7000 ft, *Blum et al. 2423* (FSU, MO, SCZ). Cerro Horqueta, 7000 ft, *Blum & Dwyer 2593* (FSU, MO, SCZ). Between Bambito and Cerro Punta, *Croat 10557* (DUKE, MO). 9 mi from Paso Cañoas, *Croat 22207* (DUKE). 1 mi E of Cañas Gordas, *Croat 22333* (DUKE, MO). Vic. of Las Nubes, 2.7 mi NW of Río Chiriquí Viejo, 2200 m, *Croat 22382* (DUKE, MO). Bajo Chorro, 6000 ft, *Davidson 33* (F, MO). Cerro Horqueta, 5000–5800 ft, *Dwyer et al. 457* (GH, MO, NY, US). Cerro Respinga on Boquete Trail, 2000–2500 m, *Gentry 5908* (MO). 7 mi S of Volcán, *Graham 256* (GH, MICH). Cerro Horqueta, 6500 ft, *von Hagen 2091* (NY). Bajo Mono trail NW of San Ramón towards the headwaters of the Río Caldera, 1600–1700 m, *Luteyn 3733* (DUKE). Bajo Chorro Trail from Paso de Respinga to Fila de Respinga, 2360–2500 m, *Luteyn 3826* (DUKE). Vic. of Boquete, 1200–1800 m, *Maurice 722* (US). 2.5 km SE of Cerro Punta, *Mori & Kallunki 5641* (DUKE, MO). N of San Félix at Chiriquí-Bocas del Toro border on Cerro Colorado copper mine road, *Mori & Kallunki 5919* (DUKE, MO). Bajo Grande, 1–3 km E of Cerro Punta, 2000–2200 m, *Nee 10063* (DUKE, MO). Vic. of Cerro Punta, 6800 ft, *Ridgway & Solis 2390* (DUKE, MO, SCZ). Near Cerro Punta, 5500 ft, *Sawyer s.n.* (MO, WIS). 3 mi S of El Volcán, 4000 ft, *Tyson 880* (FSU, MO). Bambito, 5600 ft, *Tyson 5647* (FSU, MO). 6 mi above Cerro Punta, 7500 ft, *Tyson 7153* (PMA). Valley of the upper Río Chiriquí Viejo, 1300–1900 m, *White & White 13* (GH, MO). Above Cerro Punta toward Bajo Grande in Quebrado Bajo Grande, 6500 ft, *Wilbur et al. 19013* (DUKE, MO, PMA). Above the Río Caldera beyond Bajo Mono, 1800 m, *Wilbur et al. 11080* (DUKE, F, MO). Trail between Cerro Punta and Quebrado Bajo Grande, 2000–2100 m, *Wilbur et al. 11917* (DUKE, MO). Río Chiriquí Viejo, ca. 2 mi NE of Cerro Punta, Cerro Respinga, *Wilbur & Teeri 13110* (DUKE). Quebrado Bajo Grande, ca. 2 mi E of Cerro Punta, 6900 ft, *Wilbur & Teeri 13131* (DUKE). Between the town of Cerro Punta and Las Nubes, E side of the mountain of Cerro Punta, *Wilbur & Teeri 13261* (CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, US).

S slopes of Cerro Horqueta, 5600 ft, *Wilbur et al. 13438A* (DUKE, MICH, MO), *13438B*, *13438C* (both DUKE). Above San Ramón near Bajo Mono, 4 mi NW of Boquete, 6000 ft, *Wilbur et al. 13538* (DUKE). Ca. 5 km NW of the town of Cerro Punta, 2000–2300 m, *Wilbur et al. 15204* (CR, DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Ca. 3 km WNW of Cerro Punta, 2000 m, *Wilbur et al. 15265* (DUKE, MICH, MO). SW slopes of Cerro Horqueta, ca. 6 km NW of Boquete, 1700–1800 m, *Wilbur et al. 15427* (DUKE). Upper Río Chiriquí Viejo, 2 km S of Cerro Punta, *Wilbur et al. 15333* (DUKE, MO). Near Guadelupe ca. 3.5 km from Cerro Punta, *Wilbur et al. 15354* (DUKE). Trail from Cerro Punta to Boquete, 7500 ft, *Wilbur et al. 17141* (DUKE). NE of Cerro Punta, 7200 ft, *Wilbur et al. 17150* (DUKE). Bajo Mono Trail, ca. 7 mi N of Boquete, 6000 ft, *Wilbur et al. 17242* (DUKE, MICH, MO). Between Cerro Punta and Boquete, 8200 ft, *Wilbur et al. 17251* (DUKE, F, MICH, MO). Ca. 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn 19212*, *19242* (both DUKE). 5 km NW of Cerro Punta towards Cerro Pichcho, 2000–2100 m, *Wilbur & Luteyn 19348* (DUKE). Quebrado Velo, 1800 m, *Woodson & Schery 271* (GH, MO). Vic. of Bajo Mano and Quebrada Chiquero, 1500 m, *Woodson & Schery 525* (GH, MO). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 844* (MO).

8. **Centropogon gutierrezii** (Planch. & Oerst.) F. E. Wimmer, Repert Spec. Nov. Regni Veg. 22: 202. 1926.

Siphocampylus gutierrezii Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 155. 1857. TYPE: Costa Rica, Volcán Irazú, *Oersted 9239* (C).

S. thysanopetalus Vatke, Linnaea 38: 731. 1874. SYNTYPES: Panama, Veraguas, *Warscewicz 13*, (not seen). Costa Rica, Irazú, [Trazu], *Hoffman 109* (not seen).

Herbs; stems ascendant to sprawling, hollow, to 1.2 m long, glabrate below and moderately pilose above with trichomes 0.5–1 mm long. Principal *leaves* with blades ovate-lanceolate to ovate or ovate-oblong, (5–)7–12(–14) cm long, (1.5–)2.5–5(–7) cm wide, mostly 2–3 times as long as wide, apically acute, basally cuneate to rounded, rarely almost truncate, marginally conspicuously dentate with the teeth ca. 0.5 mm long and 4–8 per cm, glabrous above except sparingly pilose on the impressed principal veins, beneath spreading pilose especially along the elevated veins; petioles ca. 1.2 cm long, moderately pilose. *Flowers* solitary in the axils of the upper leaves, 7.5–8.5 cm long; pedicels sparingly pilose, 5–12 cm long; bracteoles 2, linear, entire to sparingly dentate, pilose, 6–10 mm long, ca. 1 mm wide at the base, borne 3–8(–12) mm from the pedicel base; hypanthium sparingly pilose, 9–15 mm long in flower; calyx lobes linear or narrowly lanceolate, acute, usually obscurely toothed, somewhat pilose, 12–15(–18) cm long; corolla magenta or reddish purple, the tube 3.5–4.3 cm long, straight, narrowest at the base where about 4 mm in diameter, enlarging to the mouth where 7–10 mm in diameter, externally pilose to short-pubescent, becoming densely so above, the trichomes mostly 0.5 mm long or longer, the lobes linear, acute to acuminate with a conspicuous fringe of enlarged trichomes and corolline appendages or outgrowths 1.0–1.7 mm long, the upper 2 lobes 1.8–2.5 cm long, the lower 3 lobes 2.2–3.0 cm long; filament tube glabrous, 5–6 cm long, exserted from the corolla tube, the anthers 7–11 mm long, glabrous except for a tuft of white trichomes ca. 1.5 mm long at the tip of the 2 shortest anthers. *Berries* leathery, wide-spreading to pendent, 2.2–3.7 cm long, 1.2–1.8(–2.4) cm wide; seeds plumply lenticular, 0.6–0.7 mm long, foveate-reticulate.

This species is only known from the Costa Rican Cordillera Central and from a single collection from Cerro Panda of the Panamanian-Costa Rican Cordillera de Talamanca.

CHIRIQUÍ: Valley of the upper Río Chiriquí Viejo, Cerro Pando, *White 3* (MO).

9. **Centropogon leucocarpus** McVaugh, J. Wash. Acad. Sci. 39: 161. 1949. TYPE: Panama, *Allen 4836* (MICH, holotype; MO, US, isotypes).

Slender *herbs* ca. 80 cm tall; stems minutely puberulous throughout, sparsely so below, the trichomes minute, curving, hyaline, less than 0.1 mm long. Principal *leaves* with blades narrowly lanceolate, (3–)5–10 cm long, mostly 1–2 cm wide, ca. 4–6 times as long as wide, apically tapering to the long-attenuate tip, basally rounded to somewhat cuneate, marginally shallowly serrate-dentate with (4–)6–8 incurved, dark-tipped teeth per cm, sparsely to moderately minutely puberulous above, moderately to densely but inconspicuously so beneath, the trichomes hyaline, ca. 0.1 mm long; petioles puberulous, 0.8–1.5 cm long. *Flowers* solitary in the axils of the upper leaves, 3.4–3.8 cm long; pedicels slender, flexuous, ascending to widely spreading, ebracteolate, puberulous, 3–4 cm long; hypanthium in anthesis campanulate, basally acute, 3.5–4.5 mm long, 2.5–3 mm in diameter, inconspicuously but densely puberulous with curved trichomes ca. 0.1 mm long; calyx lobes erect, triangular, entire, 1.7–4(–5) mm long, inconspicuously puberulous; corolla red, drying purplish, externally minutely but densely puberulent with purplish trichomes less than 0.1 mm long, internally glabrous, the tube 22–25 mm long, slightly curved, basally constricted to 1.5–2 mm in diameter, gradually enlarged for the upper two-thirds to 3.5–4.5 mm in diameter, the lobes narrowly linear with slender, almost caudate tips, the upper pair of lobes erect, 9.0–11.0 mm long, the lateral lobes 8–10 mm long, the lowermost lobe 9–14 mm long; filament tube glabrous, 28–29 mm long, somewhat exserted, the anthers 4–5 mm long with the 2 lowest anthers bearing an apical tuft of stiff trichomes 0.5–1 mm long, otherwise glabrous. *Berries* globose, white, 6–8 mm in diameter; seeds ovoid-lenticular, minutely reticulate, ca. 0.5 mm long.

This species is known only from the western and southern slopes of Cerro Horqueta, Chiriquí, Panama at an elevation of 1,600–2,000 m. It is most closely related to *Centropogon luteynii* which is known only from the area west of Volcán Chiriquí.

CHIRIQUÍ: W slopes of Cerro Horqueta, 5000–7000 ft, *Allen 4836* (MICH, MO, US). S flank of Cerro Horqueta, 1750–2100 m, *Cochrane et al. 6274* (MO). S slopes of Cerro Horqueta, 5000–6000 ft, *Wilbur et al. 17310* (DUKE). Slopes approaching Cerro Horqueta on ridge 6.6 mi NNE of Boquete, 1800 m, *Wilbur & Luteyn 19326* (DUKE, MICH, MO).

10. **Centropogon luteynii** Wilbur.[14] TYPE: Panama, *Wilbur et al. 17163* (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, US, isotypes).

Slender, straggly, terrestrial *herbs* to ca. 70 cm tall; stems densely but minutely and inconspicuously puberulent on young growth but soon sparse or glabrate, the trichomes slightly spreading and curving upward and inward, ca.

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[14] *Centropogon luteynii* Wilbur, sp. nov. Herba tenuis, erecta puberula 50–70 cm alta. Lamina foliorum ovata vel lance-ovata, (2–)4–8(–9.5) cm longa et 2–5 cm lata, 2–2.5-plo longior quam latior, marginis dentatis; nervis brevissme puberulis. Pedicelli ebracteolati, puberuli (2–)3–5(–6) cm longi. Lobi calycis erecti, triangulari, 3–6 mm longi. Corolla rubra vel coccinea, puberula; tubi 2.3–2.7 cm longi; lobi lineari, non falcati, 6–10 mm longi. Filamenta 27–30 mm longa; tubus antherarum penicillatus.

0.1 mm long. Principal *leaves* with blades ovate to lance-ovate, mostly (2–)4–8 (–9.5) cm long, 2–5 cm wide, ca. 2–2.5 times as long as wide, apically acute to acuminate, basally cordate, marginally conspicuously dentate with usually 6–9 (–13) dark purple-tipped teeth per cm, the teeth 0.5–0.7 mm long, glabrous or nearly so on the upper surface, the puberulence, when present, restricted to the principal veins, the pubescence of the lower surface persisting and copious but inconspicuous and restricted to the elevated veins, the trichomes minute, curved, mostly less than 0.1 mm long; petioles puberulous, (0.5–)1–2 cm long. *Flowers* solitary in the axils of the upper leaves, 3.5–4.0 cm long; pedicels slender, flexuous, ascending to widely spreading, ebracteolate, sparingly to moderately but inconspicuously puberulous, (2–)3–5(–6) cm long; hypanthium in anthesis cylindric-campanulate, basally rounded, 3–5 mm long, 2–3 mm in diameter, moderately to densely but inconspicuously puberulent, the appressed incurved trichomes ca. 0.1 mm long; calyx lobes erect or with the tip slightly spreading or recurving, narrowly triangular, entire, 3–6 mm long, glabrous or sparingly puberulent; corolla bright red or crimson externally, paler within, drying dark purplish, externally inconspicuously puberulous with hyaline or reddish trichomes less than 0.1 mm long, glabrous internally, the tube 2.3–2.7 mm long, slightly curved, basally constricted to 1.5–2.5 mm in diameter, gradually enlarging in the upper two-thirds to ca. 4–6 mm in diameter, the lobes all narrowly linear and erect to somewhat spreading, the upper pair erect, 7–10 mm long, the lateral pair 6–9 mm long and cut more deeply on the ventral than on the dorsal margin, the lowermost lobe 5–8 mm long; filament tube glabrous, reddish, 27–30 mm long, slightly exserted, the anthers 4–5 mm long, the 2 lowest anthers bearing an apical tuft of stiff, white bristles 0.8–1.0 mm long, otherwise glabrous. *Berries* globose to oblong, 8–14 mm long, 8–12 mm in diameter; seeds lenticular, orbicular, minutely foveate-reticulate, ca. 0.5 mm long, dark brownish.

This species is known only from wet mountain slopes and streambanks northwest of Cerro Punta in Chiriquí Province at 1,800–2,160 m.

CHIRIQUÍ: Above Las Nubes, NW of Cerro Punta, 1900–2100 m, *Luteyn 3799* (DUKE). Trail beyond Las Nubes to midway between Cerro Picacho and Cerro Punta, 1900–2200 m, *Luteyn & Wilbur 4629* (DUKE, MICH), *4638* (DUKE). Las Nubes region, 2–5.5 km NW of Cerro Punta and 2 km NW of Las Mirandes, 2000–2410 m, *Utley et al. 251* (DUKE). Vic. of Las Nubes, ca. 6 km NW of the town of Cerro Punta, 6000–7200 ft, *Wilbur et al. 17105* (DUKE, F, MICH, MO), *17163* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US). Ravine W of Las Nubes towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19355* (CAS, DUKE, F, GH, LL, MICH, MO, NY, US), *19358* (DUKE, F, MICH, MO, US).

11. **Centropogon panamensis** Wilbur.[15] TYPE: Panama, *Wilbur et al. 15611* (DUKE, holotype; F, GH, LL, MICH, MO, NY, PMA, US, isotypes).—FIG. 3.

Coarse, erect, little-branched *shrubs* 1–2.5 m tall; stems hollow, glabrous below the inflorescence, becoming woody basally, to 2 cm in diameter. Median

[15] *Centropogon panamensis* Wilbur, sp. nov. Frutex vel suffrutex erectus, 1–2.5 m altus. Lamina foliorum elliptica vel oblonga, (10–)15–25(–33) cm longa et 6–12 cm lata, nervis brevissme inconspicue spiculata-papillata. Racemus 5–15(–30) cm longus, pedunculatus, erectus; bracteae 1.5–3(–6) cm longae et 0.5–1(–2) cm latae; pedicelli 0.5–1.5(–2) cm longi,

FIGURE 3. *Centropogon panamensis* Wilbur.—A. Habit (×3/5).—B. Anther tube and top of filament tube. (×3 3/10). [After *Wilbur et al. 15611* (DUKE).]

cauline *leaves* with blades broadly elliptic, oblong or ovate or obovate, (10–) 15–25(–33) cm long, mostly 6–12 cm wide, 1.5–2.5 times as long as wide, drying relatively thick and more or less chartaceous, apically acute to acuminate, basally tapering into a petiole 0.5–1.5(–2) cm long, marginally irregularly and incon-

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puberuli. Lobi calycis erecti, acuti, 5–11(–16) mm longi, spiculati. Corolla rosea vel carminea, spiculata vel brevissime hirtella; tubus 3.0–3.3 cm longus, valde curvata, faux inflatum, 10–12 (–14) mm diametro; lobi superiores revoluti, 8–12 mm longi, acuti; lobi laterali falcati, 4–8 mm longi. Filamenta exserta, 35–38 mm longa; antherarum tubus cornutus, 6–8 mm longus, in conmissuris 3 dorsalibus albido- vel lilacino pilosus.

spicuously callose-denticulate with 3–6 white to pale yellow, rounded denticulations per cm, dark green and glabrous above, minutely granular-papillate beneath along the principal veins, otherwise glabrous. *Inflorescences* 5–15(–30) cm long, few to 25-flowered in a more or less densely umbellate or racemose terminal cluster; peduncle usually dark brownish, short-pubescent (1–)5–10(–15) cm long; bracts greatly reduced, foliaceous, often 1.5–3(–6) cm long, 0.5–1(–2) cm wide. *Flowers* 5–6 cm long; pedicels densely spiculate to minutely short-pubescent, 0.5–1.5(–2) cm long; bracteoles 2, linear, 2–4 mm long borne about 1–5 mm above the pedicel base; hypanthium moderately to densely spiculate-pubescent, basally more or less broadly rounded, 5–8 mm high; calyx lobes erect, dark green, narrowly triangular, acute, entire to minutely and irregularly toothed, moderately to densely spiculate-pubescent on both surfaces, 5–11(–16) mm long; corolla bright pink or roseate, densely short-spiculate externally with minute sharply conical stiff trichomes 0.1–0.2 mm long, glabrous internally, the tube 3.0–3.3 cm long, abruptly bent just above the middle, 4–6 mm in diameter below the bend and flaring above to 10–12(–14) mm in diameter at the throat, the 2 upper lobes reflexed, 8–12 mm long, acute, the 2 lateral lobes falcate, deltoid, 4–8 mm long, acute, the lowermost lobe 5–7 mm long, erect, acute; filament tube 35–38 mm long, glabrous to slightly hairy at the apex, white, barely exserted, the anther tube 6–8 mm long with a dense bearded line of violet, lavender to whitish, straight, stiff trichomes mostly 0.8–1.2 mm long along the back in the connective groove between the 3 upper anthers, the 2 lower anthers glabrous or more sparingly hirsute along their connectives but with a concrescent, stiff, triangular scale 1.5–2.5 mm long and with a dense fringe of erect, stiff trichomes external to the cornute scale. *Berries* leathery, subglobose, 12–15 mm in diameter; seeds lenticular, foveate-reticulate.

Centropogon panamensis is known from wet mountain slopes in Panama. It is readily distinguished from *C. granulosus*, a species with which it has been confounded in the past. *Centropogon granulosus* is a sprawling vine with pendent, elongate inflorescences, while *C. panamensis* is an erect shrublet with congested, erect inflorescences.

BOCAS DEL TORO: Río Teribe, near Quebrado Lukulon, 300 ft, *Kirkbride & Duke 515* (MO). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 2026* (DUKE, MO). CANAL ZONE: 5 mi E of Ferry Thatcher Bridge, *Lazor 3305* (FSU, SCZ). COCLÉ: Vic. of El Valle, 800–1000 m, *Allen 211* (MO). Vic. of El Valle, 600–1000 m, *Allen 1213* (MO). Vic. of La Mesa, N of El Valle de Antón, 1000 m, *Allen 2392* (AA, MO, US). Hills N of El Valle de Antón, trail to La Mesa, 1000 m, *Allen 2709* (MO, US). N of El Valle de Antón, 700–800 m, *Allen 4217* (MO). El Valle, on trail to Cerro Pilón, *Correa 51* (SCZ). 2.5 mi above El Valle on road to La Mesa, *Croat 13371* (MO). La Mesa above El Valle de Antón, *Croat 14368* (DUKE, MO). Cerro Pilón near El Valle, 700–900 m, *Duke 12102* (MO); *Duke & Correa 14656* (MO, REED). El Valle, *Dwyer 1928* (MO). El Valle de Antón at foot of Cerro Pilón, 2000 ft, *Dwyer & Correa 7992* (MO). La Mesa, 4 km N of El Valle, 875 m, *Nee & Dwyer 9173* (DUKE, MO). La Mesa above El Valle, *Dwyer & Nee 11923* (MO). Vic. of La Mesa, N of El Valle, 1000 m, *Gentry 6849* (DUKE, MO). El Valle de Antón, along Río Indio Trail, 500–700 m, *Hunter & Allen 299* (MO). El Valle WEPCOR site, *Kirkbride 1083* (MO). Cerro Pilón, *Lallathin 6002* (MO, PMA). N of El Valle de Antón, 2500–3000 ft, *Lewis et al. 1760* (MO). Cerro Pilón, 900–1173 m, *Liesner 776* (MO). 5 mi N of El Valle de Antón, 1000 m, *Luteyn 1184* (DUKE). 5 mi NW of El Valle de Antón, 1000 m, *Luteyn 1227* (DUKE). Ca. 8 mi N of El Valle de Antón, *Luteyn & Kennedy 1680* (DUKE, MICH). Trail to Las Minas, N of El

Valle de Antón, 800–900 m, *Luteyn 3159* (DUKE). La Mesa, NW of El Valle de Antón, 850–900 m, *Luteyn 4077* (DUKE). Foot of Cerro Pilón, El Valle de Antón, *Porter et al. 4421, 4625* (both MO). El Valle to La Mesa, *Spellman et al. 581* (MO). La Mesa, 5 mi N of El Valle, 2500 ft, *Tyson & Godfrey 2430* (FSU, NY, SCZ). La Mesa above El Valle de Antón, 1000 m, *Weaver & Foster 1644* (DUKE, MICH). La Mesa, *Wilbur et al. 11108* (DUKE, F, MO, NY, PMA, US). Trail to La Mesa, ca. 4.5 mi beyond El Valle de Antón, *Wilbur & Luteyn 11689* (DUKE). Near La Mesa, ca. 5 mi N of El Valle, *Wilbur & Luteyn 11732* (DUKE). W slopes of Cerro Pajita ca. 3 mi N of El Valle, *Wilbur et al. 15611* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US). La Mesa, in the crater of El Valle de Antón, 850 m, *Wilbur et al. 15640* (DUKE, F, LL, MICH, MO). DARIÉN: Río Tacarcuna, vic. of old Tacarcuna village, 580 m, *Gentry & Mori 13568* (MO). PANAMÁ: Cerro Campana, 2300 ft, *Blum et al. 2373* (FSU, MO, SCZ). Cerro Campana, *Croat 12091* (MO). Road to Cerro Campana, *Croat 14708A* (MO). Cerro Campana above Su Lin Motel, *Croat 14745* (MO). 3 mi NE of Altos de Pacora, 500–800 m, *Croat 22728* (DUKE). Cerro Jefe beyond Goofy Lake, *Duke 8006* (MO, REED). Cerro Campana above Su Lin Motel, *Dwyer & Kirkbride 7856* (MO). Cerro Campana, *Ebinger 330* (F, MICH, MO, US); *Garner 24* (DUKE, SCZ); *Gentry 4919* (MO); *Hayden 115* (MO); *Lewis et al. 1910* (DUKE, MO). 8.6 mi SW of Capira on Cerro Campana, *Luteyn 977* (DUKE, MICH). Cerro Campana, *Luteyn & Kennedy 1788* (DUKE); *McDaniel 6861* (DUKE, FSU, MO); *Mori & Kallunki 3558* (DUKE, MO). 5–10 km NE of Altos de Pacora, ca. 750 m, *Mori & Kallunki 4949* (MO). Cerro Campana above Su Lin Motel, *Porter et al. 4176* (DUKE, MO). Cerro Campana, ca. 2500 ft, *Tyson & Lazor 6234* (PMA); *Wilbur & Weaver 11285* (DUKE, F, MO, PMA, US). VERAGUAS: Cerro Tuté, vic. of Santa Fé, *Allen 4349, 4368* (both MO). 5 mi W of Santa Fé, 800–1200 m, *Croat 22984* (DUKE). Río Primero Brazo, 2.5 km beyond Escuela de Alto Piedra near Santa Fé, 700–750 m, *Croat 25481* (MO). Valley of Río Dos Bocas between Alto Piedra and Calovebora, 350–400 m, *Croat 27379* (MO). 3.9–5 mi N of Santa Fé, 500–1000 m, *Gentry 2967* (MO). Above Río Primero Brazo, 5 mi NW of Santa Fé, *Liesner 834* (MO). Road beyond Escuela Agrícola de Alto Piedra above Santa Fé, 800–1000 m, *Luteyn & Wilbur 4577* (DUKE). N of Santa Fé, 2 km N of Escuela Agrícola, *Mori & Kallunki 2630* (MO). Río Dos Bocas, 11 km from Escuela Agrícola, *Mori & Kallunki 3081* (MO). NW of Santa Fé and 11 km from Escuela Agrícola in valley of Río Dos Bocas, 450–550 m, *Mori et al. 3837* (MO). 6–7 km W of Santa Fé, 2900 ft, *Nee 9734, 9792* (both DUKE, MO). Ca. 2 km N of Santa Fé, *Wilbur & Luteyn 19123* (CAS, DUKE, F, MICH, MO, NY, US).

12. **Centropogon smithii** F. E. Wimmer, Ann. Naturhist. Mus. Wien 46: 240. 1933. Based on *Siphocampylus discolor*.

Siphocampylus discolor Donnell Smith, Bot. Gaz. (Crawfordsville) 23: 248. 1897, non *C. discolor* Kunth & Bouché ex Kunth, Ann. Sci. Nat. Bot., sér. 3, 9: 316. 1848. TYPE: Costa Rica, Volcán Barba, *Tonduz* (Herb. Inst. Nat. Costaric. *2149*) (US, lectotype; CR, isolectotype).

Robust, unbranched, erect *shrubs* 1–3.5 m tall; stems mostly simple, hollow, glabrous below and short pubescent above. *Leaves* clustered in a palmlike terminal rosette; blades of the principal leaves obovate to oblanceolate to broadly elliptic, (10–)15–36 cm long, 6–10(–15) cm wide, usually 2–4 times as long as wide, apically abruptly narrowed to a short deltoid-acuminate tip, basally cuneate or tapering into a stout petiole 1–3.5 cm long, marginally somewhat sinuate, subentire to denticulate, the teeth often 0.3–0.6 mm long and dark purplish, glabrate or sparsely scurfy near the base on the upper surface, the lower surface with dense scurfy emergences. *Flowers* 6–8 cm long; pedicels solitary in the upper leaf axils, scurfy or glabrate, 11–24 cm long; bracteoles narrowly linear, scurfy, basal, spreading, denticulate, 1–2 cm long; hypanthium scurfy; calyx lobes linear-subulate to narrowly triangular, scurfy, denticulate, 1.8–3.3 cm long; corolla cream to pale greenish white, or yellowish, the lobes often purple or purple flecked,

externally scurfy, internally glabrous, the tube 1.9–2.1 cm long, narrowest medially, the lobes falcate, attenuate, strongly recurved, the 2 upper lobes 2–4 cm long, the 3 lower lobes 1.6–2.5 cm long; filament tube (3.1–)4.0–4.7 cm long, the upper half softly pubescent, the anther tube 13–15 mm long, the 2 shorter anthers with a dense tuft of white hairs, all basally pilose but otherwise glabrous. *Berries* depressed-globose, (1.5–)2–3.5 cm in diameter, surmounted by a free rim of the hypanthium 2–6 mm high; seeds slightly longer than wide, flattened, foveate-reticulate.

In Panama this species is known only from a single collection. It is also known from Costa Rica in the Talamancas and in the Cordillera Central.

This species is a large, palmiform shrub to 3.5 m tall with greenish white or cream-colored flowers 6–8 cm long. The corollas are of a burmeisteroid aspect and the unpleasant odor of the crushed leaves and flowers is very reminiscent of certain species of the genus *Burmeistera*. *Centropogon smithii* is the sole Central American representative of the distinctive South American section *Burmeisteroides* Gleason which is composed of about 15 species (McVaugh, 1949).

CHIRIQUÍ: Recently opened ravine west of Las Nubes, ca. 5 km NW of Cerro Punta towards Cerro Picacho, 2000–2100 m, *Wilbur & Luteyn 19352* (DUKE, F, MICH, MO).

3. DIASTATEA

Diastatea Scheidw., Allg. Gartenzeitung 9: 396. 1841. TYPE: *D. virgata* Scheidw.

Annual *herbs*; roots fibrous; stems erect. *Leaves* simple, exstipulate, alternate, sessile to shortly petiolate, pinnately veined and usually serrate to dentate. *Inflorescences* loosely racemose, slightly to strongly secund, the flowers inverted at anthesis; pedicels filiform, spreading-ascendant, often upturned, ebracteolate, borne in the axils of foliaceous bracts. *Flowers* with the hypanthium shallowly cup shaped to obconic; calyx lobes linear, triangular, elliptic or lanceolate; corolla bilabiate, purplish blue to pale or white, glabrous, the tube entire, not dorsally slit, persistent, greatly stretched by the expanding capsule and then becoming scarious and hyaline; filaments equalling or slightly exceeding the corolla tube, connate above but below free from one another and loosely adnate to the corolla tube, the anthers unequal in size with the 2 shorter apically minutely white-tufted, the 3 longer usually apically glabrous. *Capsules* superior or nearly so with not more than ⅓ its length fused to the hypanthium, dehiscing loculicidally and apically, usually erect or nearly so, bilocular with axile placentation; seeds numerous, ellipsoid, smooth and shining, 0.5–0.6 mm long.

This is a genus of 5 species which ranges from Mexico south through Central America and through the Andean region of South America to Bolivia and Peru.

Literature:

McVaugh, R. 1940. A revision of "Laurentia" and allied genera in North America. Bull. Torrey Bot. Club 67: 778–798. [*Diastatea*, pp. 784–794.]

1. **Diastatea micrantha** (H.B.K.) McVaugh, Bull. Torrey Bot. Club 67: 143. 1940.—Fig. 4.

Lobelia micrantha H.B.K., Nov. Gen. Sp. Pl. 3: 316. 1819. TYPE: Ecuador, in the vicinity of Quito near Puembo, *Humboldt & Bonpland* (not seen).
L. subtilis H.B.K., Nov. Gen. Sp. Pl. 3: 317. 1819. TYPE: Ecuador, in the vicinity of Quito near Puembo, *Humboldt & Bonpland* (not seen).
L. ruderalis Willd. ex R. & S., Syst. Veg. 5: 56. 1819. TYPE LOCALITY: Peru.
L. draba Willd. ex R. & S., Syst. Veg. 5: 67. 1819. TYPE: not seen.
Rapuntium micranthum (H.B.K.) Presl, Prodr. Monogr. Lobel. 25. 1836.
R. subtile (H.B.K.) Presl, Prodr. Monogr. Lobel. 25. 1836.
Lobelia parviflora Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles 9(2): 41. 1842. TYPE: Mexico, Oaxaca, *Galeottii 1970* (BR, not seen).
L. minutiflorum Kunze, Linnaea 16: 318. 1842.
Laurentia ovatifolia B. L. Robinson, Proc. Amer. Acad. Arts 26: 166. 1891. TYPE: Mexico, Jalisco, *Pringle 2985* (GH, not seen).
L. michoacana B. L. Robinson, Proc. Amer. Acad. Arts 26: 166. 1891, pro syn.
L. michoacana var. *ovatifolia* B. L. Robinson, Proc. Amer. Acad. Arts 26: 166. 1891, pro syn.
Lobelia türckheimii Vatke ex B. L. Robinson, Proc. Amer. Acad. Arts 26: 166. 1891, pro syn.
Dortmannia micrantha (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 972. 1891.
D. minutiflora (Kunze) Kuntze, Rev. Gen. Pl. 2: 972. 1891.
D. parviflora (Mart. & Gal.) Kuntze, Rev. Gen. Pl. 2: 973. 1891.
Laurentia micrantha (H.B.K.) Zahlbr., Bull. Torrey Bot. Club 24: 386. 1897, non A. DC. (1839).
L. pedunculata Brandegee, Univ. Calif. Publ. Bot. 6: 73. 1914. TYPE: Mexico, Chiapas, *Purpus 6705* (UC, holotype: not seen).
L. maximiliana F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 78. 1935. SYNTYPES: Mexico, Guerrero, *Schultze 163, 113* (B, neither seen).
L. micrantha var. *longibracteata* F. E. Wimmer, Revista Sudamer. Bot. 2: 104. 1935. TYPE LOCALITY: Brazil and Paraguay.
Laurentia micrantha var. *ovatifolia* (B. L. Robinson) F. E. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13(6): 476. 1937.
?*Diastatea maximiliana* (F. E. Wimmer) F. E. Wimmer, Ann. Naturhist. Mus. Wien 56: 332. 1948.
Diastatea micrantha var. *longibracteata* (F. E. Wimmer) F. E. Wimmer, Ann. Mus. Naturhist. Mus. Wien 56: 332. 1948.
Diastatea micrantha var. *ovatifolia* (B. L. Robinson) F. E. Wimmer, Ann. Mus. Naturhist. Mus. Wien 56: 332. 1948.

Annual *herbs* 5–50(–75) cm tall; stems simple or branched, often purplish, terete to angled, sometimes narrowly winged and chaffy-pubescent to glabrous. Principal *leaves* chartaceous to more typically membranous, lanceolate to ovate, sessile to distinctly petiolate, the petiole to 13 mm long with the pubescence, if present, mostly concentrated on the margins, on the veins of the lower surface and on the base of the upper surface, serrate, serrulate, sinuate or jagged-toothed; blades mostly 2.2–5.5 cm long, (0.5–)1–3 cm wide. *Inflorescences* somewhat secund, few- to 30-flowered; pedicels (6–)15–30(–42) mm long, usually upturned distally, glabrous, ciliate or chaffy-hirsute. *Flowers* 4.5–6.5(–8) mm long; calyx tube mostly glabrous, 0.5–1 mm high, the calyx lobes linear, entire or sparingly ciliate-toothed, 1.5–3.5(–5.5) mm long and less than 0.5 mm wide at the base, acute to acuminate apically; corolla dark purplish blue, pale lilac, blue, or rarely white, the tube 2.5–4 mm long, the 2 upper lobes broadly triangular, ca. 1.5 mm long, the 3 lower lobes rounded-spatulate, ca. 2 mm long; filaments 3–4.5 mm long, the anther tube 0.5–1.5 mm long, the 3 longest anthers apically glabrous and externally often sparingly short-pubescent, the 2 shorter anthers with a dense fringe

FIGURE 4. *Diastatea micrantha* (H.B.K.) McVaugh.—A. Habit (×⅗).—B. Capsule with persistent corolla and stamens (×5⅗). [After *Wilbur et al. 15578* (DUKE).]

of short bristles ca. 0.2 mm long. *Capsules* 3–6(–8) mm long, 1.5–2.5 mm in diameter, narrowly ellipsoid.

Diastatea micrantha is found in fields, pastures, roadsides, open woods, and disturbed sites mostly at 1,000 to 2,700 m. It ranges from Central Mexico (San Luis Potosí and Jalisco) southward through the Central American highlands and through the Andes from Colombia to Peru and Bolivia. It is probably more common than the number of collections would indicate; it grows in weedy sites and is easily overlooked.

CHIRIQUÍ: Vic. of Boquete, 3300–4200 ft, *Lewis et al. 356* (GH, MO, US). COCLÉ: Vic. of El Valle, 600–1000 m, *Allen 1155* (GH, MO, NY). PANAMÁ: Pacora, *Killip 3321* (US). Road at El Valle de Antón, outer rim of the crater, *Wilbur et al. 15578* (DUKE, MICH, MO).

4. HIPPOBROMA

Hippobroma G. Don, Gen. Syst. 3: 717. 1834. TYPE: *H. longiflora* (L.) G. Don.

Lobelia sect. *Solenanthis* H.B.K., Nov. Gen. Sp. Pl. 3: 309. 1819. TYPE: *L. longiflora* L.
Isotoma sect. *Solenanthis* (H.B.K.) A. DC., Prodr. 7: 412. 1839.

Coarse perennial *herbs*; roots tuberous, fleshy. *Leaves* simple, exstipulate, alternate, short-petiolate, pinnately veined and both repand-dentate and denticulate. *Flowers* solitary in the axils of undifferentiated leaves; pedicels short, basally bibracteolate, more or less erect at anthesis; hypanthium obconic, strongly 10-ribbed; calyx tube extending above the ovary as a narrow free rim; calyx lobes erect, linear; corolla salverform, white, the tube entire, the lobes equal or nearly so, much shorter than the tube; filaments equalling or somewhat exceeding the corolla tube, connate distally but distinct from one another from just below the apex of the corolla tube to the base, adnate to the corolla tube, the anthers connate, all white-beared at the apex but otherwise glabrous, conspicuously unequal in length; stigma broadly and strongly bilobed. *Capsules* pendent at maturity, ⅘ inferior or more, biloculate, dehiscing loculicidally and apically; seeds plump, cylindric with broadly rounded ends, minutely foveolate-reticulate.

Hippobroma is a monotypic genus.

Literature:

McVaugh, R. 1940. A revision of "Laurentia" and allied genera in North America. Bull. Torrey Bot. Club 67: 778–798. [Hippobroma, pp. 782–784.]

1. **Hippobroma longiflora** (L.) G. Don., Gen. Syst. 3: 717. 1834.—FIG. 5.

Lobelia longiflora L., Sp. Pl. 930. 1753. TYPE: Jamaica.
Rapuntium longiflorum (L.) Miller, Gard. Dict., ed. 8. *Rapuntium* No. 7. 1768.
Isotoma longiflora (L.) Presl, Prodr. Monogr. Lobel. 42. 1836.
Laurentia longiflora (L.) F. E. Wimmer, Field Mus. Nat. Hist., Bot. Ser. 13: 474. 1937, non *L. longiflora* Schlecht., 1922.

Erect or decumbent *herbs* (15–)30–50(–90) cm high; stems short-pubescent to nearly glabrous. *Leaves* sessile, membranous, elliptic to oblanceolate, coarsely and irregularly repand-dentate with 15–20 large teeth as well as callose-dentic-

FIGURE 5. *Hippobroma longiflora* (L.) G. Don. Habit (×7/10). [After *Wilbur & Luteyn 19090* (DUKE).]

ulate with 4–6 times as many small teeth, mostly (5–)10–20 cm long, (1–)2–5 cm wide, apically acute, basally cuneate. *Flowers* with the pedicels 4–8 mm long bearing almost basally a pair of filiform bracteoles 2–4 mm long; hypanthium 6–10 mm long, obconic, angulate, strongly 10-ribbed, spreading short-pubescent; calyx lobes linear, erect, 10–18(–22) mm long, ca. 1 mm wide, marginally callose-denticulate, spreading short-pubescent, rarely glabrous; corolla white to white with pale greenish veins, puberulous, the tube 5–13.5 cm long, (1–)2–4 mm in diameter, the lobes subequal, spreading, 1.3–2.7 cm long, elliptic-lanceolate; filament tube glabrous, the anther tube slightly curved, the shorter anthers ca. 3 mm long, the longer anthers about 5–6 mm long. *Capsules* 1.2–2.0 cm long,

pendent, often appearing more completely inferior than they actually are due to the closely enveloping free rim of the hypanthium; seeds ca. 0.8 mm long.

Hippobroma longiflora is common in the West Indies which apparently was its original home and from Mexico south into Brazil and Peru. It has been sparingly introduced into the Old World tropics.

This plant is reputedly extremely poisonous as suggested by its generic name which translates as "horse poison." It has also been reported that the sap causes severe inflammation to the eyes or even blindness.

BOCAS DEL TORO: No locality, *Carleton 156* (US). Region of Almirante, *Cooper 123* (F, MICH). RR track near station at Milla 5, *Croat & Porter 16491* (MO). Changuinola Valley, *Dunlap 49b* (F). Runway at Bocas, *Lazor et al. 2403* (MO). Changuinola to 5 mi S at junction of Ríos Changuinola and Terebé, 100–200 ft, *Lewis et al. 811* (GH, MO, US). Chiriquicito to 5 mi S along Río Guarumo, *Lewis et al. 1953* (DUKE, MO). Almirante, *McDaniel 5073* (MO). Changuinola to 5 mi S at junction of Ríos Changuinola and Terebé, 100–200 ft, *Oliver 811* (NY). Vic. of Chiriquí Lagoon, *von Wedel 1116* (GH, MO, US). Water Valley, Chiriquí Lagoon, *von Wedel 1701* (GH, MO, US). CANAL ZONE: Pipeline Road near Gamboa, *Clewell & Tyson 3310* (FSU, MO, PMA). Frijoles, *Croat 10371* (MO). Fort Kobbe, *Duke 3945* (MO). 1 mi S of the Summit Gardens, *Lazor & Blum 5344* (SCZ). Pipeline Road, N of Gamboa, *Luteyn & Foster 1540* (DUKE, F). Navy Reservation, N of Gamboa, *Robyns 65–41* (GH, MO). Ancón Hill, *Seibert 105* (GH, MO, NY). Vic. of Río Cocolí near bridge, *Stern et al. 318* (GH, MO). Pipeline Road, NW of Gamboa, *Wilbur & Teeri 11315b* (DUKE, F, GH, MICH, MO). CHIRIQUÍ: 12 mi W of Puerto Armuelles, 400–500 m, *Liesner 213* (MO). COCLÉ: Boca del Toabré at confluence of Río Toabré and Río Coclé del Norte, *Lewis et al. 5536* (MO). El Valle de Antón, *Wilbur & Luteyn 11712* (DUKE, MO). COLÓN: Road to Santa Rita, 250 m, *Busey & Mahler 334* (DUKE, MO). Portobelo, *Chan 52* (MO); D'Arcy *4061* (MO). Santa Rita Hills, *Smith 3440* (F). 5–7 mi SW of Portobelo towards María Chiquita, *Wilbur & Weaver 11196* (DUKE, MO). Portobelo, *Wilbur & Luteyn 11656* (DUKE). HERRERA: Road between Las Minas and Pesé, 600 ft, *Duke 12308* (MO). 12 mi S of Ocú, *Graham 231* (GH, MICH); *Lewis et al. 1640* (MO). 10 mi S of Ocú, *Tyson et al. 2868* (SCZ). 1 mi N of Las Minas and 14 mi S of Ocú, *Wilbur et al. 12116* (DUKE). PANAMÁ: Chagres River between Juan Mina and Madden Dam, *Bartlett & Lasser 16493* (MICH, MO). Cerro Azul, *Castrejon 38* (PMA). Road between Goofy Lake at Cerro Azul and main highway, *Correa & Dressler 435* (SCZ). Cerca del Río Chagres, *Díaz 31* (F, PMA). Piriá, 150 m, *Duke 14420* (REED). Goofy Lake, *Dwyer et al. 4140* (DUKE, MO). Santa Rosa, a orillas del Río Chagres, *Escobar 16* (PMA). Alrededores de Chilibre, *González 18* (MO, PMA). Isla Taboga, *Hjerting & Rahn 621* (C). Chimán, *Lewis et al. 3338* (DUKE, MO, PMA). Sabanas NE of Panama City, *Paul 170* (US). Villa Rosario, *Saldana 8* (DUKE, MO, PMA). Tumba Muerto Road, near Panamá, *Standley 29808* (US). Juan Díaz, *Standley 30523* (US). SAN BLAS: Río Ailigandí, *Duke 10829* (REED). VERAGUAS: Cerro de Tute, 1000 ft, *Dwyer 4287* (MO, SCZ, US). Ca. 1 km N of Santa Fé, *Wilbur & Luteyn 19090* (DUKE).

5. LOBELIA

Lobelia L., Sp. Pl. 929. 1753; Gen. Pl., ed. 5. 401. 1754.

Dortmanna Hill, Brit. Herb. 126. 1756.
Rapuntium Miller, Gard. Dict., ed. 8. 1768.
Tupa G. Don. Gen. Syst. 3: 700. 1834. TYPE: *T. feuillei* G. Don = *Lobelia tupa* L.
Dortmannia Steud., Nom. Bot., ed. 2. 1: 526. 1840.
Petromarula Nieuwl. & Lunell ex Lunell, Amer. Midl. Naturalist 5: 1917, non 1806.

Annual or perennial *herbs* or *shrubs*. *Leaves*, simple, exstipulate, alternate, sessile or short-petiolate, pinnately veined and serrate to subentire with the teeth ending in minute callosities. *Flowers* solitary in the terminal leaf axils or in

bracted, terminal racemes, usually inverted, pedicellate, mostly bibracteolate, more or less ascendant at anthesis; corolla usually with a dorsal slit from the apex nearly to the base and often bearing 2 lateral slits (= fenestrae) as well, strongly zygomorphic with 2 upper lobes and 3 lobes comprising the lower lip; filaments usually free from the corolla, connate at least distally into a monodelphous tube, the anthers laterally united into a tube and the pollen released into the central cavity formed by the fused anthers, unequal, the 2 lower anthers shorter, usually with a penicellate tuft of bristles at the tip, the 3 longer anthers partially closing the orifice of the anther tube by their strongly incurved tips. *Capsules* ¼ to completely enclosed by the hypanthium, dehiscing loculicidally apically, corolla, stamens and style withering-persistent; seeds, numerous, smooth and shining, pitted or tuberculate.

This is a large and heterogenous genus of more than 350 species.

Literature:

McVaugh, R. 1940a. Campanulaceae (Lobelioideae). Pp. 347–353 *in* R. E. Woodson, Jr. & R. W. Schery, Contributions toward a flora of Panama. IV. Ann. Missouri Bot. Gard. 27: 265–364.

———. 1940b. A key to the North American species of *Lobelia* (Sect. *Hemipogon*). Amer. Midl. Naturalist 24: 681–702.

———. 1958. *Lobelia splendens* Humb. & Bonpl. ex Willd., a poorly understood member of the *Lobelia cardinalis* complex. Bol. Soc. Bot. México 23: 48–54.

a. Corolla scarlet, red, reddish orange, pinkish, reddish yellow or pale greenish; corolla tube 10 mm long or more.
  b. Corolla pale greenish; bracteoles more than 5 mm long and 1 mm wide, borne well above the middle of the pedicel ..... 2. *L. dressleri*
  bb. Corolla red, orange, pinkish or rarely white; bracteoles less than 5 mm long and 1 mm wide, borne near the middle of the pedicel or well below it.
    c. Bracteoles at or near the base of the pedicels; pedicels 2 cm long or less; seeds roughened, foveate-reticulate; herbs ..... 1. *L. cardinalis*
    cc. Bracteoles usually at or near the middle of the pedicels but occasionally nearly basal, minute and apparently often wanting; pedicels (1–)3 cm long or more; seeds more or less smooth with faint longitudinal lines; shrubs or suffrutescent herbs ..... 5. *L. laxiflora*
aa. Corolla blue or violet blue or pale lavender to almost white; corolla tube 5 mm long or less.
  d. Corolla tube 2.5 or less; anther tube 1 mm long or less; annuals.
    e. Mature capsule ⅓ inferior or less; fruiting pedicels 10 mm long or longer ..... 7. *L. xalapensis*
    ee. Mature capsule nearly completely inferior; fruiting pedicels 2–6 mm long ..... 3. *L. fastigiata*
  dd. Corolla tube 2.8 mm long or longer; anther tube 1 mm long or longer; perennials.
    f. Corolla tube fenestrate, 2.8–3 mm long, blue to violet; lower corolla lobes 4–6 mm long; upper corolla lobes triangular, 3–6 mm long; all 5 anthers minutely white-tufted at tips ..... 4. *L. irasuensis*
    ff. Corolla tube nonfenestrate, 3–4 mm long, pale lavender to white; lower corolla lobes 2–3.5 mm long; upper corolla lobes nearly linear, 2.0–3.2 mm long; only the 2 shorter anthers apically minutely white-tufted ..... 6. *L. longicaulis*

1. **Lobelia cardinalis** L., Sp. Pl. 930. 1753.

Herbs 0.4–1.5(–2.0) m tall, usually perennating by offsets; stems erect and unbranched, glabrous to densely pubescent. Cauline *leaves* 10–30, spreading, relatively thin or papery when dried, glabrous to densely short-pubescent, subentire to coarsely beset with callose-tipped teeth, linear, lanceolate, oblong or ovate, usually apically acute, basally tapering or the lower leaves with a petiole to 3 cm long. *Inflorescences* 15–30(–50) cm long, not especially secund, with few–100, loose to densely clustered flowers 3–5 cm long; pedicels more or less erect, slender, 4–15(–20) mm long, glabrous, spiculate, or short-pubescent, basally bibracteolate, the filiform bracteoles mostly 1–2 mm long, subtended by linear and small, sometimes leafy bracts; hypanthium conic to campanulate, glabrous to densely spreading short-pubescent, mostly 8–11 mm in diameter; calyx lobes entire, linear, glabrous or stiffly ciliate especially basally, 8–16(–20) mm long; corolla scarlet, deep crimson or red, or rarely pink to white, usually externally puberulent, the lip glabrous, the tube usually 15–20 mm long, fenestrate, the upper 2 corolla lobes linear, erect, 13–20 mm long, 1–2 mm wide, the 3 lower lobes deflexed, ovate, acute, 13–20 mm long, (2–)3–4(–9) mm wide; filaments 19–33 mm long, longer than the corolla tube, glabrous to densely spreading short-pubescent, connate distally for more than half their length, the anther tube bluish gray, the 2 shorter anthers 2.2–2.7 mm long, bristly white-tufted with trichomes 0.8–1.2 (–1.5) mm long, the 3 longer anthers 3.5–4.5(–5.5) mm long, glabrous to moderately bristly pubescent. *Capsules* about half interior, usually 6–8(–10) mm high; seeds linear-oblong, light brown, 1.0–1.2 mm long.

The only element found in southern Central America according to McVaugh (1942) is subsp. *graminea* (Lam.) McVaugh var. *graminea*. Fortunately this greatly simplifies identification for the varieties are by no means easy to distinguish in areas in which several seem more or less sympatric.

1a. **Lobelia cardinalis** subsp. **graminea** (Lam.) McVaugh var. **graminea**

L. graminea Lam., Encycl. Méth. 3: 583. 1791.
L. splendens Willd., Hort. Berol. *pl. 86*. 1809.
Rapuntium gramineum (Lam.) Presl, Prodr. Monogr. Lobel. 26. 1836.
R. splendens (Willd.) Presl, Prodr. Monogr. Lobel. 26. 1836.
Lobelia ignea Paxton, Paxton's Mag. Bot. 6: 247. 1839.
L. splendens var. *atro-sanguinea* Hook., Bot. Mag. *pl. 4002*. 1843.
L. fulgens var. *glabriuscula* Walp., Repert. Bot. Syst. 2: 707. 1843. Based on *L. splendens* Willd.
L. splendens var. *ignea* (Paxton) Hook., Bot. Mag. *pl. 4960*. 1857.
Dortmannia graminea (Lam.) Kuntze, Rev. Gen. Pl. 2: 972. 1891.
D. splendens (Lam.) Kuntze, Rev. Gen. Pl. 2: 973. 1891.

Herbs, glabrous or very nearly so. Principal cauline *leaves* linear to narrowly lanceolate, 9–15(–22) cm long, 0.4–1.5(–2.5) cm wide, usually 10–14 times as long as wide, entire or nearly so. *Inflorescences* many-flowered with rather leafy bracts resembling and in close proximity to the foliage leaves.

This taxon is distributed from Central Mexico south into Panama.

CANAL ZONE: Madden, *Dwyer & Robyns 9a* (MO). Chiva-Chiva Trail, 2 mi above Red Tank, *Maxon & Harvey 6577* (GH, NY, US). Chiva-Chiva Trail, Red Tank to Pueblo Nuevo,

Piper 5721 (US). Across from Albrook Research Forest Site, *Rankin s.n.* (SCZ). Chiva-Chiva Trail, 2 mi W of Miraflores Lake, *Tyson & Blum 3564* (FSU, MO, SCZ). Vic. of Miraflores Lake, *White 155* (MO). CHIRIQUÍ: Chiriquí, Boquete District, *Davidson 818* (F, MO). Río Caldera S of El Boquete, 1250 m, *Killip 3619* (US). David airport, *Lewis et al. 762* (GH, MO). Vic. of Boquete, 1200–1500 m, *Woodson & Schery 728* (GH, MO). Finca Lérida to Boquete, 1300–1700 m, *Woodson et al. 1096* (GH, MO, NY). COCLÉ: Vic. of El Valle de Antón, ca. 600 m, *Allen 1984* (MO). Near falls of Río Antón, *Allen 2775* (GH, MO, US). Road to El Cope from Interamerican Highway, *Burch et al. 1379* (MO). 12 mi NE of Penonomé, 1200 ft, *Lewis et al. 1517* (DUKE, MO). 1 mi W of El Valle de Antón, *Luteyn 1272* (DUKE, F). Vic. of Olá, 100–350 m, *Pittier 5030* (C, US). Penonomé and vic., 50–1000 ft, *Williams 219* (NY, US). HERRERA: Vic. of Ocú, *Stern et al. 1745* (MICH, MO, US). 4 mi S of Los Pozos, *Tyson 2663* (FSU, SCZ). 5 mi S of Ocú, *Wilbur 12093* (DUKE). PANAMÁ: Chiva-Chiva Trail to Search Light Station, *Allen 951* (GH, MO, NY, US). La Ermita, San Carlos, *Bernal 19* (DUKE, PMA). Chiva-Chiva River, *Killip 3132* (MO, US). Along stream of the Río Teta near Pan-American Highway, *Luteyn 1574* (DUKE, F). 1 mi N of Goofy Lake, *Oliver et al. 2567* (DUKE, MO). Sabanas, *Paul 49* (US). Between Las Sabanas and Matías Hernández, *Standley 31824* (US). VERAGUAS: La Yeguada, Camino de Altos de la Gallota a Cerro Verde, 1000 m, *Correa et al. 1956* (DUKE). San Francisco, *Dwyer 1296* (FSU, GH, SCZ). 15 mi N of Calobre, 644 m, *Luteyn 1437* (DUKE). Along stream near Santa Fé, ca. 1700 ft, *Luteyn 4044* (DUKE).

2. **Lobelia dressleri** Wilbur, Ann. Missouri Bot. Gard. 61: 889. 1974. TYPE: Panama, *Dressler 4206* (DUKE, holotype; PMA, isotype).

Suffruticose *herbs* to 1 m tall; stems basally to 5 cm in diameter, apparently unbranched or nearly so and inconspicuously spreading short-pubescent. *Leaves* cauline, apparently numerous and rather evenly spaced along the stem, spreading-ascendant, thin papery to semichartaceous when dry, inconspicuously serrulate with appressed, incurved teeth, medially 1–3 per cm; blades elliptic, slightly broadest above the middle, acutely tapering both apically and basally, 15–30 cm long, 3–7.5 cm wide, about 4–6 times as long as wide, glabrous on both the upper and lower surfaces; petioles glabrous, 1–2 cm long. *Inflorescences* 60–80 cm long, 40–70-flowered, narrowly cylindrical; bracts elliptic, tapering to either end and somewhat broader above the middle, inconspicuously serrulate, glabrous, the upper bract ca. 2 cm long, 6–8 mm wide, the lowermost bract to 10 cm long, 3–4 cm wide; pedicels stiff, straight, strongly divaricate except distally where upturned at anthesis and somewhat incurved in fruit, 1.2–2.8 cm long in flower, 2–3 cm long in fruit, 1–1.5 mm in diameter, densely spreading short-pubescent and bearing a pair of linear to lanceolate, serrulate, glabrous bracteoles ca. ¾ or more the distance from the base of the pedicel, 6–10 mm long, 1–2 mm wide. *Flowers* 2.8–3.2 cm long including the hypanthium; hypanthium at anthesis broadly hemispherical, glabrous or basally spreading short-pubescent, symmetrical or nearly so, 6–9 mm high, 10–15 mm in diameter, with a free calycine rim about 2 mm high; calyx lobes at anthesis triangular or deltoid, glabrous, inconspicuously serrulate, 5–8 mm long, 2–4 mm wide at the base; corolla light green, glabrous, the tube 10–15 mm long, distally strongly curved ventrally, dorsally slit, at first to within 6–8 mm and eventually to within 1 mm of the base and with 2 conspicuous lateral fenestrae (slits) 4–6 mm high, the lobes all strongly arching ventrally, the 2 upper lobes linear or linear-lanceolate, 10–15 mm long, ca. 2 mm wide, acute, the 3 lower lobes 8–12 mm long, 2 mm wide; filament tube glabrous, 15–20 mm long, connate except for the basal 4–5 mm, the anther tube 4–6 mm long, glabrous

except for the dense tuft of white trichomes ca. 1 mm long at the apex of each anther. *Capsules* somewhat depressed hemispheric, 8–12 mm high, 10–15 mm in diameter, ca. ⅔ superior, terminating in the tapering, 2–4 mm long, conical base of the style; seeds compressed, broadly oblong, ca. 0.8 mm long, 0.6 mm broad, shallowly pitted.

Lobelia dressleri is known only from two collections made in Colón Province, both near the beach. This species belongs to Section *Tylomium* (Presl) Benth. & Hook. characterized by shallowly pitted seeds, nonbluish flowers, nonbasal and conspicuously bibracteolate pedicels, and a stoutly herbaceous or subshrubby habit. The 20 or so species of this section range in the Caribbean from the Greater Antilles south through the Lesser Antilles and perhaps onto Trinidad. On the mainland its species are known from northern Central America, Guatemala, Honduras and probably Nicaragua, and from Panama.

COLÓN: Near Coclé del Norte, near beach, *Dressler 4206* (DUKE, PMA). Miguel de la Borda along beach, *Croat 10016* (DUKE, MO).

3. **Lobelia fastigiata** H.B.K., Nov. Gen. Sp. Pl. 3: 313. 1819. TYPE: Ecuador, *Humboldt & Bonpland* (not seen).

L. tenuifolia Willd. ex R. & S., Syst. Veg. 5: 56. 1819. TYPE: not seen.
Rapuntium fastigiatum (H.B.K.) Presl, Prodr. Monogr. Lobel. 15. 1836.
Lobelia trinitensis Griseb., Fl. Brit. W. Ind. 385. 1861. TYPE LOCALITY: Trinidad.
L. gardneriana Kanitz in Martius, Fl. Bras. 6(4): 138. 1878. TYPE: not seen.
Dortmannia trinitensis (Griseb.) Kuntze, Rev. Gen. Pl. 2: 380. 1891.
D. fastigiata (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 972. 1891.
D. gardneriana (Kanitz) Kuntze, Rev. Gen. Pl. 2: 972. 1891.

Erect annual *herbs* 15–40 cm tall; stems glabrous or nearly so. Principal *leaves* with blades narrowly lanceolate to ovate-lanceolate, marginally sinuate-serrate with 3–10 widely spaced teeth on each side, 0.5–2.5(–4.0) cm long, 5–8 mm wide, usually 3–6 times as long as wide. *Inflorescences* not secund, loosely few- to 20-flowered, the flowers appearing solitary in the axils of the upper leaves or bracts; pedicels slender, 2–6 mm long, varying from bristly to granular-roughened to nearly glabrous, basally bibracteolate with oblong to spatulate bracteoles 0.5–1 mm long. *Flowers* with the hypanthium glabrous, campanulate to somewhat obconical in anthesis; calyx lobes linear to lanceolate, entire, 2–3 mm long in flower and 5–6 mm long in fruit, glabrous to slightly granular; corolla 3–5 mm long, pinkish, glabrous, the tube ca. 2 mm long with the dorsal slit extending nearly to the base, nonfenestrate; filaments ca. 2 mm long, distally connate; anther tube 0.2–0.7(–1.0) mm long with a fringe of white bristles ca. 0.1 mm long at the apex of the 2 lowermost anthers, the anthers otherwise glabrous except for sparse, short pubescence on the backs of the uppermost anthers. *Capsules* almost completely inferior, 5–6 mm long; seeds ellipsoid, smooth, shining.

This species is widely distributed in South America from Paraguay and southern Brazil north to Central Panama and Trinidad.

PANAMÁ: Wet field between Matías Hernández and Juan Díaz, *Standley 32038* (US).

4. **Lobelia irasuensis** Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 153. 1857. TYPE: Costa Rica, Volcán Irazú, 8000 ft, *Oersted 9246* (C, holotype, US, photo).

L. warscewiczii Vatke, Linnaea 38: 718. 1874. TYPE: Costa Rica or Panama, *Warscewicz 20* (B, holotype, not seen; US, photo).
Dortmannia warscewiczii (Vatke) Kuntze, Rev. Gen. Pl. 2: 973. 1891.

Perennial *herbs* with tuberous fleshy roots; stems erect or decumbent, 8–35 (–56) cm tall, glabrous, sparsely short-pubescent or scabridulous below. Principal *leaves* with blades firm, linear to linear-lanceolate, the lowermost sometimes oblong, apically acuminate, basally rounded to tapering, often somewhat subclasping and sessile, 1–3(–5) cm long, 2–5(–8) mm wide, usually (3–)7–12(–15) times as long as wide. *Inflorescences* loosely few- to 30-flowered, often somewhat secund; pedicels ascendant to erect, slender, usually spreading short-pubescent, 4–6(–9) mm long; bracteoles usually present, basal, knoblike or oblong to linear-filiform, 0.5–1.5 mm long. *Flowers* 8–14 mm long; hypanthium minutely short-pubescent, especially basally, cup shaped and somewhat oblique at anthesis; calyx lobes linear to narrowly triangular, 2–5 mm long, often callose-serrate, sparingly appressed short-pubescent especially near base of the upper surface; corolla glabrous or nearly so, deep blue or purplish, usually with conspicuous creamy markings near base of the 3 lower lobes, the tube 2.8–3.0 mm long, usually fenestrate, the 2 upper lobes oblong-spatulate to linear or triangular, 3–6 mm long, the 3 lower lobes elliptic to oblong-spatulate, 3–6 mm long and 2.5–3.5 mm wide; filaments ciliate and distinct for most of their length but apically connate into a tube 1–2 mm long, the anther tube 1.0–1.3 mm long, all anthers minutely apically white-tufted. *Capsules* ½–¾ inferior, 3–5 mm long; seeds ca. 0.5 mm long, dull to somewhat lustrous with faint longitudinal markings.

Lobelia irasuensis is found on the highest mountains of Costa Rica and western Panama mostly above 3,000 m.

McVaugh (1943: 62) considered this species to be composed of three varieties with only the type variety occurring in Costa Rica and Panama and the other two restricted to central Mexico.

CHIRIQUÍ: Volcán Chiriquí, 10400 ft, *Davidson 1006* (F, GH, MO, US). Chiriquí Volcano, El Potrero Camp, 2800–3000 m, *Pittier 3072* (GH, US). Valley of the upper Río Chiriquí Viejo, *White 59a* (MO). Potrero Muleto to summit, Volcán Chiriquí, 3500–4000 m, *Woodson & Schery 407* (GH, MO). Potrero, Loma Larga to summit, Volcán Chiriquí, 2500–3380 m, *Woodson et al. 1031* (GH, MO, NY).

5. **Lobelia laxiflora** H.B.K., Nov. Gen. Sp. Pl. 3: 331. 1819. TYPE: not seen.

Straggly *shrubs* or coarsely suffrutescent perennial *herbs* (0.2–)0.8–1.5(–3.0) m tall, stems glabrous to densely short-pubescent at least above. Principal *leaves* with blades glabrous to densely pubescent, subentire to more typically finely and evenly beset with callose-tipped serrations, linear-lanceolate to broadly elliptic or ovate, 4–12(–25) cm long, (0.5–)1.5–3.5(–4.5) cm wide, mostly 3–6(–10) times as long as wide, apically acute to acuminate, basally cuneate or rarely rounded. *Inflorescences* terminal with (10–)20–60 flowers axillary to the bracts or the upper reduced leaves, mostly 15–30(–60) cm long. *Pedicels* 1–10 cm

long, stiffly ascendant to loosely spreading, glabrous to somewhat villous, bibracteolate medially or to within 3–4 mm of the base, the filiform bracteoles 0.5–1.5 mm long. *Flowers* 2.7–4.8 cm long; hypanthium glabrous or pubescent, campanulate or shallowly cup-shaped in flower, becoming broadly hemispheric in fruit; calyx lobes (1–)3–4(–6.5) mm long, entire, shortly deltoid, narrowly triangular to linear, glabrous or pubescent; corolla red, orange, or yellowish, externally glabrous to densely short-pubescent, the tube 1.6–2.5 mm long, fenestrate, the upper 2 lobes linear, 1–2 cm long, the lower lobes largely fused into a linear-oblong lip 1.0–1.8 cm long bearing 3 acute teeth 1–3(–10) mm long; filaments glabrous to densely spreading short-pubescent, connate above for about ⅔ their length, (1.8–)2.2–2.7(–3.5) cm long, the anther tube (5–)6–7(–9) mm long, the 2 shorter anthers apically densely white-tufted with stiff trichomes, the 3 longer anthers apically moderately villous-hirsute or occasionally appressed villous throughout. *Capsules* more than half inferior, 5–10 mm high; seeds ellipsoid or oblong, nearly smooth but with faint longitudinal lines, 0.6–0.8 mm long.

Lobelia laxiflora ranges from Baja California and southern Arizona south through Mexico and Central America into northwestern South America (Colombia). The variety *stricta* ranges from central Mexico (Jalisco and Michoacán) southward as far as Colombia and is apparently the only variant found south of Guatemala.

5a. **Lobelia laxiflora** var. **stricta** (Planch. & Oerst.) McVaugh.—Fig. 6.

L. rigidula H.B.K., Nov. Gen. Sp. Pl. 3: 311. 1819. TYPE: Probably from Mexico (not seen).
Rapuntium rigidulum (H.B.K.) Presl, Prodr. Monogr. Lobel. 26. 1836.
Lobelia ovalifolia Hook. & Arn., Bot. Beech. Voy. 300. 1838. TYPE: *Beechey* (not seen).
L. angulato-dentata Hook. & Arn., Bot. Beech. Voy. 301. 1838. TYPE: *Beechey* (K, not seen).
L. floribunda Bonpl. ex. A. DC., Prodr. 7: 383. 1839, pro syn.
L. ? *andina* Benth., Pl. Hartw. 213. 1845. TYPE: *Hartweg 1183* (K, not seen).
Siphocampylos mollis Regel, Flora 33: 353. 1850. TYPE: Described from a cultivated plant, originally collected in Guatemala by Warscewicz (not seen).
S. *warscewiczii* Regel, Schweiz. Z. Gartenbau 8: 143. 1850. Based on S. *mollis* Regel, 1850, not S. *mollis* Planch, 1850–1851.
Tupa costaricana Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 154. 1857. TYPE: Costa Rica, *Oersted 9245* (C, lectotype).
T. costaricana var. *stricta* Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 155. 1857. TYPE: Costa Rica, *Oersted 9245* (C, lectotype).
T. costaricana var. *patula* Planch. & Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1857: 155. 1857. TYPE: Costa Rica, vicinity of San José or Cartago, *Oersted* (not seen).
Lobelia persicaefolia var. *mollis* (Regel) Vatke, Linnaea 38: 722. 1874.
L. persicaefolia var. *warscewiczii* (Regel) Vatke, Linnaea 38: 723. 1874.
L. patzquarensis Ses. & Moc., Pl. Nov. Hisp. 152. 1890. TYPE: Mexico (MA, not seen).
L. laxiflora var. *brevifolia* Zahlbr., Repert. Spec. Nov. Regni Veg. 14: 185. 1915. TYPE: *Lehmann 4674.*
L. laxiflora var. *foliosa* Zahlbr., Repert. Spec. Nov. Regni Veg. 14: 185. 1915. TYPE: *Lehmann 3656*, (US, isotype).
L. laxiflora var. *mollis* (Regel) Zahlbr., Repert. Spec. Nov. Regni Veg. 14: 185. 1915.
L. costaricana (Planch. & Oerst.) F. E. Wimmer, Ann. Naturhist. Mus. Wien 46: 239. 1933.
?*L. costaricana* var. *magna* F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 85. 1935. TYPE: Mexico, *Hegewisch* (GOET, not seen).
L. rensonii F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 38: 85. 1935. TYPE: El Salvador, near San Salvador, *Renson 54* (NY, holotype, not seen).

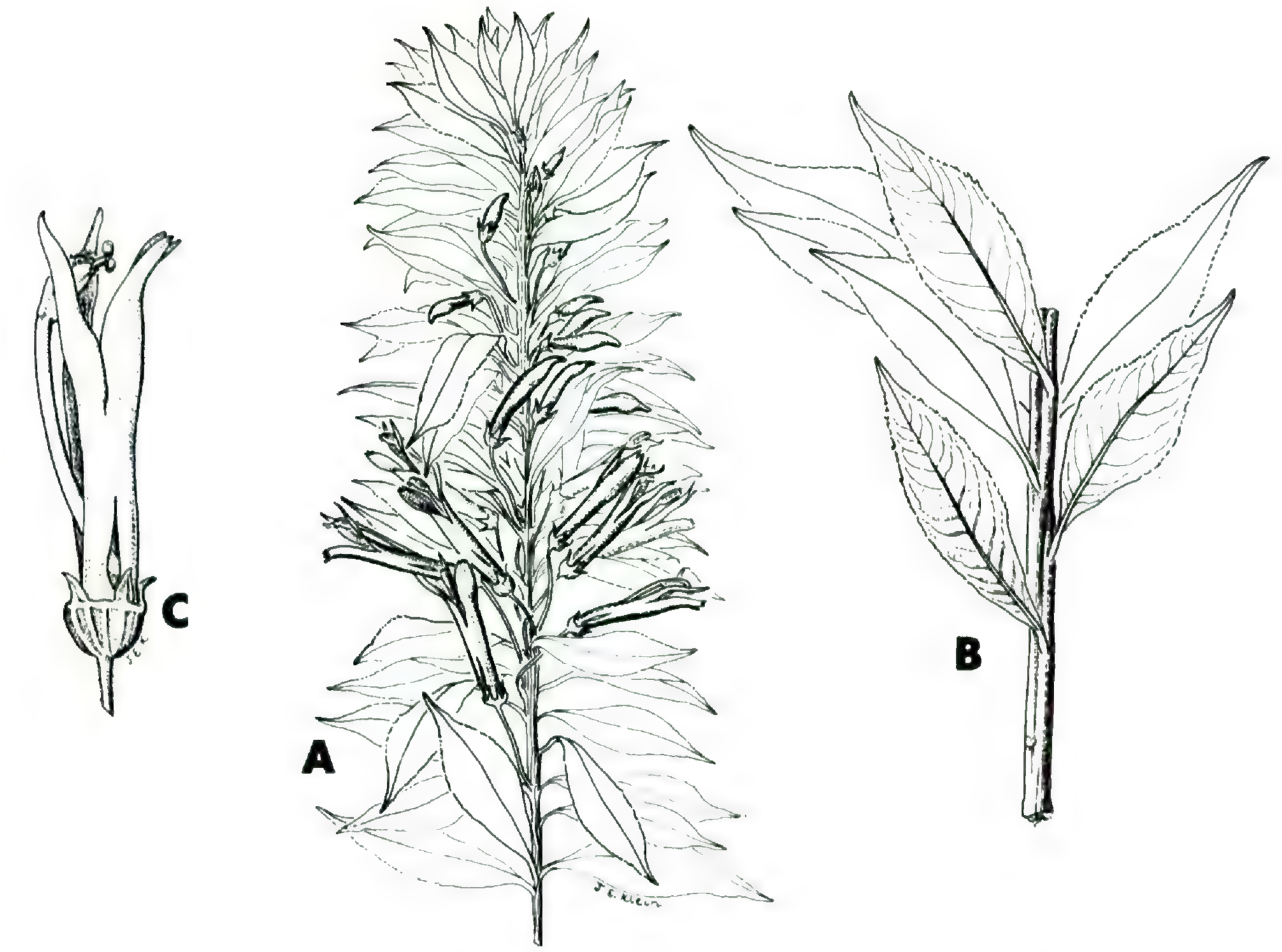

FIGURE 6. *Lobelia laxiflora* var. *stricta* (Planch. & Oerst.) McVaugh.—A. Habit (×⅖).—B. Stem and leaves (×⅖).—C. Flower (×1⅒). [After *Luteyn 1488* (DUKE).]

L. haenkeana var. *panamensis* F. E. Wimmer, Ann. Naturhist. Mus. Wien 56: 368. 1948. TYPE: Panama, *Pittier 2869* (US, holotype).

Plants usually densely pubescent. Principal leaves 4–10(–17) cm long, 1.5–3 (–4.5) cm wide, usually 3–5 times as long as wide. Pedicels stiff, straight, closely appressed to the stem at least at its base.

Lobelia laxiflora var. *stricta* ranges from west-central Mexico and Guatemala south into Colombia.

CHIRIQUÍ: Volcán de Chiriquí, 1200 m, *Allen 991* (MO). Ca. 5 km NW del Hato del Volcán, *Correa 1374* (DUKE, PMA). Boquete, 4500–6000 ft, *Davidson 1* (F). Bajo Mono, 4500 ft, *Davidson 518* (F, GH, MO). Volcán de Chiriquí, 7000 ft, *Davidson 891* (F, GH). Near Volcán, ca. 4600 ft, *Duke 9145* (MO, US). Between Boquete and Cerro Horqueta, *Duke 13716* (SCZ). Volcán Barú, 3400 m, *Gutiérrez s.n.* (PMA). Boquete, 1450 m, *Killip 3553* (US). Vic. of Boquete, 3300–4200 ft, *Lewis 377* (GH, MO, US). 5 mi N of Boquete, *Luteyn 1479* (DUKE, GH, MICH, MO). 6.7 mi W of Boquete, 8000 ft, *Luteyn 1488* (DUKE, F, MICH, MO). Ca. 1.5 mi NE of El Hato del Volcán, 1500 m, *McDaniel 10182* (FSU). Between Bajo and Alto Lino, vic. of Boquete, 960 m, *Maurice 714* (MO, US). Barú, ca. 2500 m, *Mori & Bolten 7362* (MO). W slopes of Volcán Chiriquí, 1500 m, *Mori & Kallunki 5689* (DUKE, MO). Vic. of Boquete, 3300–4200 ft, *Oliver 377* (NY). Around El Boquete, 1000–1300 m, *Pittier 2869* (US). Just S of Boquete, 3500 ft, *Stern et al. 1931* (MICH, MO, US). 8 mi NE El Volcán, 8100–8400 ft, *Tyson 839* (FSU, MO). W slope of El Barú, 6000–7000 ft, *Tyson & Loftin 5949* (DUKE, FSU). Cerro Punta, ca. 6000 ft, *Tyson 7133* (PMA). Valley of the Upper Chiriquí Viejo, Cerro Panda, *White 40* (MO). Río Chiriquí Viejo Valley, *White 78* (GH, MO). Río Chiriquí Viejo Valley near El Volcán, *White 236* (GH, MO). NE of El Hato del Volcán, near Aguacate, 1800–1900 m, *Wilbur et al. 10985* (DUKE, F, GH, MO,

NY, PMA, US). 3 mi NW of Boquete below Bajo Quiel, *Wilbur et al. 12032* (DUKE, GH, MO). Between Volcán de Chiriquí and Cerro Aguacate, 6500–7200 ft, *Wilbur & Teeri 13320* (DUKE, F, MO, MICH). Ca. 4 mi NW of Boquete, 4200 ft, *Wilbur et al. 13511* (DUKE, MICH). Between El Hato and Volcán de Chiriquí, *Wilbur et al. 15404* (DUKE). Ca. 4 mi NW of Boquete, 1350 m, *Wilbur et al. 15521* (DUKE, MO). Río Caldera, ca. 2 mi up-river from Boquete, *Wilbur et al. 17253* (DUKE). Above the Río Caldera, ca. 3 km beyond Bajo Mono, 1500 m, *Wilbur & Luteyn 19203* (DUKE). 3 km S of Bambito and 4.2 km N of El Hato del Volcán, 1400–1600 m, *Wilbur & Luteyn 19415* (DUKE). Casita Alta, Volcán de Chiriquí, 1500–2000 m, *Woodson et al. 872* (GH, MO, NY). Finca Lérida to Peña Blanca, 1750–2000 m, *Woodson & Schery 301* (GH, MO). COCLÉ: Vic. of El Valle, 600–1000 m, *Allen 1779* (GH, MO, NY, US). 3 km E of El Valle de Antón at km 21, 725 m, *Nee & Hale 9665* (MO). Ca. 7 km S of El Valle de Antón, *Wilbur & Luteyn 11703* (DUKE, F, MO, PMA, US). 3–6 km SE of El Valle de Antón, *Wilbur & Luteyn 11752* (DUKE, GH, MO). PANAMÁ: Ca. 5 mi SE of El Valle, *Wilbur et al. 15577* (DUKE).

6. **Lobelia longicaulis** Brandegee, Univ. Calif. Publ. Bot. 6: 73. 1914. TYPE: Mexico, Chiapas, *Purpus 6705* (UC, holotype, not seen).

L. neglecta Vatke, Linnaea 38: 720. 1874, non R. & S., Syst. Veg. 5: 36. 1819. TYPE: Mexico, *Ehrenberg 520* (B, not seen).
Dortmannia neglecta (Vatke) Kuntze, Rev. Gen. Pl. 2: 973. 1891.
Lobelia urticifolia F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 22: 195. 1926. Based on *L. neglecta* Vatke.
L. poasensis F. E. Wimmer, Ann. Naturhist Wien 46: 239. 1933. TYPE: Costa Rica, Volcán Poás, *Cufodontis 605* (W, holotype, not seen, AA, US, photos).

Perennial *herbs*; caudex short, woody; stems ascendant to decumbent, sparingly chaffy-pubescent, 15–50 cm long. Principal cauline *leaves* with blades ovate to broadly lanceolate or elliptic, apically acute or short-acuminate, basally rounded to more typically cuneate, marginally coarsely and irregularly serrate with 2–5 teeth per cm, sparingly chaffy-pubescent, especially on the principal veins, 2.5–8 cm long, (0.5–)1.0–4.2 cm wide, 2–6(–9) times as long as wide, nearly sessile or on narrowly winged petioles to 1 cm long. *Flowers* few –25, solitary in the axils of the upper leaves or bracts; pedicels glabrous or minutely prickly to sparsely chaffy-pubescent, ebracteolate, 0.8–2.0(–3.0) cm long; hypanthium conical, often 10-nerved, glabrous to minutely prickly or chaffy-pubescent; calyx lobes linear, entire, stiffly ciliate on both margins and often on the midvein beneath or nearly glabrous, (1.6–)3.0–4.0 mm long; corolla pale lavender to nearly white, glabrous to minutely pubescent externally, the tube 3–4 mm long, nonfenestrate but with a dorsal slit, the 2 upper lobes narrowly linear from a triangular base, 2.0–3.2 mm long, the 3 lower lobes elliptic to oblong, 2–3.5 mm long; filaments pubescent below and usually glabrous above, (2.5–)3.5–4.5 mm long, connate for about the upper third and adnate to the corolla tube for ca. 0.7 mm, the anther tube 1.0–1.6 mm long, the 2 shorter anthers minutely white-tufted, the 3 longer anthers externally stiffly and sparingly short-pubescent. *Capsules* ca. ⅓–⅔ inferior, 5.5–10 mm long; seeds ellipsoid, smooth, shining.

This species grows from central Mexico to western Panama, mostly at 600–900 m.

CHIRIQUÍ: W slopes of Volcán de Chiriquí, 2500–3400 m, *Mori & Kallunki 5758* (DUKE, MO). Potrero Muleto to summit, Volcán de Chiriquí, 3500–4000 m, *Woodson & Schery 471* (MO). Finca Lérida to Boquete, ca. 1300–1700 m, *Woodson et al. 1119* (GH, MO, NY). Bajo Chorro Trail, 5900–6200 ft, *Wilbur & Luteyn 17280* (DUKE).

7. **Lobelia xalapensis** H.B.K., Nov. Gen. Sp. Pl. 3: 315. 1819. TYPE: Mexico, near Jalapa and Maculteped, *Humboldt & Bonpland* (not seen).

L. monticola H.B.K., Nov. Gen. Sp. Pl. 3: 316. 1819. TYPE: New Granada, in mountains between Fusagasuga and Pandi, *Humboldt & Bonpland* (not seen).
L. palmaris Willd. ex R. & S., Syst. Veg. 5: 56. 1819.
L. mollis Graham, Edinburgh New Philos. J. 8: 185. 1829.
Rapuntium affine Presl, Prodr. Monogr. Lobel. 25. 1836, nom. nud.
R. xalapense (H.B.K.) Presl, Prodr. Monogr. Lobel. 25. 1836.
R. monticolum (H.B.K.) Presl, Prodr. Monogr. Lobel. 25. 1836.
R. molle (Graham) Presl, Prodr. Monogr. Lobel. 30. 1836.
Lobelia ocimoides Kunze, Linnaea 24: 178. 1851. TYPE: Mexico, *Ehrenberg* (not seen).
L. cliffortiana var. *xalapensis* (H.B.K.) A. Gray, Syn. Fl. N. Amer. 2: 7. 1878.
Dortmannia mollis (Graham) Kuntze, Rev. Gen. Pl. 2: 972. 1891.
D. monticola (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 972. 1891.
D. ocimoides (Kunze) Kuntze, Rev. Gen. Pl. 2: 973. 1891.
D. xalapensis (H.B.K.) Kuntze, Rev. Gen. Pl. 2: 973. 1891.
D. cliffortiana var. *xalapensis* (H.B.K.) Kuntze, Rev. Gen. Pl. 3(2): 187. 1898.

Erect annual *herbs* (5–)10–40(–60) cm tall; stems usually sparsely chaffy-pubescent below; roots fibrous. Principal *leaves* with blades usually slightly longer than broad, ovate, marginally sinuate as well as coarsely toothed, mostly 1–3(–5.5) cm long, 0.5–2(–4.5) cm wide, apically acute, basally rounded to cordate; petioles 0.5–3 cm long, chaffy-pubescent. *Inflorescences* not secund, often corymbose when young, few- to 40-flowered, pedunculate; pedicels slender, mostly 10–15 mm long at maturity, minutely but densely prickly puberulent, basally bibracteolate with knoblike bracteoles 0.1–0.2 mm long; bracts usually linear to filiform, 2–12 mm long. *Flowers* 4–6(–7) mm long; hypanthium prickly-puberulent but becoming glabrate especially in fruit, shallowly cupuliform in anthesis, 0.8–1.2 mm high; calyx lobes linear-subulate, entire, 2–4 mm long, glabrous or marginally ciliate; corolla pale blue to violet varying to white or even purplish, the tube externally glabrous, internally sparingly pubescent, ca. 2.5 mm long, dorsally slit to approximately 1 mm from the base but not fenestrate, the 2 upper lobes erect, ca. 1.5 mm long, the 3 lower lobes rounded and coalesced into a lip 1.5–2 mm long; filament tube 2–2.5 mm long, glabrate, connate for about the upper third, the anther tube 0.5–1 mm long, gray, the 3 longer anthers either glabrous or bristly short-pubescent near the apex, the 2 shorter anthers with a thin fringe of apical bristles ca. 0.1 mm long, otherwise either glabrous or sparingly to moderately short-pubescent. *Capsules* ⅓ inferior or less, 4–5.5 mm long, 2–3 mm in diameter; seeds ellipsoid, brown, smooth, highly polished, ca. 0.5 mm long.

Lobelia xalapensis is a widespread weedy species ranging from Vera Cruz to Oaxaca and thence throughout Central and South America into northern Argentina; it is also known from the Lesser Antilles and the Galapagos Islands.

BOCAS DEL TORO: Changuinola Valley, *Dunlap 505* (F, US). CHIRIQUÍ: Boquete, 3800 ft. *Davidson 451* (F, GH, MO, US). Vic. of Boquete, 3300–4200 ft, *Lewis et al. 335* (GH, MO, US). Vic. of Boquete, 990 m, *Maurice 691* (US). Río Caldera beyond Bajo Mono, 1700 m, *Wilbur et al. 11051* (DUKE, MO). Ca. 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn 19310* (DUKE). COCLÉ: Mountains beyond La Pintada, 400–600 m, *Hunter & Allen 554* (MO). La Mesa, 5 mi N of El Valle, 2500 ft, *Tyson & Godfrey 2470* (SCZ). PANAMÁ: 2–3 mi S of Goofy Lake, 2000–2200 ft, *Lewis et al. 231* (GH, MO, US). VERAGUAS: Ca. 2 km N of Santa Fé, *Wilbur & Luteyn 19099* (DUKE).

6. SIPHOCAMPYLUS

Siphocampylus Pohl, Pl. Bras. Icon. Descr. 2: 104. 1831. TYPE: *Lobelia westiniana* Billb. = *Siphocampylus westianus* (Billb.) Pohl.

Coarse *herbs* or *shrubs*. *Leaves* simple, exstipulate, alternate, petiolate, and usually serrate or dentate. *Flowers* axillary in the upper leaves or reduced bracts, usually inverted at anthesis, borne on bibracteolate or ebracteolate pedicels; hypanthium obconic to cylindric, adnate to the pistil for at least ⅘ of its length; corolla red, red and yellow, or red tinged with green or white, rarely blue, the tube entire or basally fenestrate, never dorsally cleft; filaments basally distinct and either adnate to the narrow basal portion of the corolla (continental species) or free from it (West Indian species), the anther tube with the opening partially closed by the incurved tips of the 3 longer anthers, the 2 shorter anthers bearing a bristly fringe of stiff white hairs. *Capsules* apically loculicidally dehiscent with a conical apex and either papery or woody walls; corolla, stamens and style withering-persistent; seeds numerous, ovoid or ellipsoid, foveate-reticulate.

This is a genus of perhaps 200 species mostly from Andean South America but with about a dozen species in the Greater Antilles, and four little collected taxa in Costa Rica and Panama.

a. Calyx lobes entire.
   b. Leaves thick and somewhat leathery when dry, about 2 times as long as wide; calyx lobes oblong; corolla lobes white, the tube fenestrate; filament tube 30 mm long or longer; Coclé Province ..... 1. *S. albiguttur*
   bb. Leaves thinly membranous when dry, ca. 3–4 times as long as wide; calyx lobes linear; corolla lobes yellow, the tube nonfenestrate; filament tube less than 30 mm long; Darién Province ..... 2. *S. darienensis*
aa. Calyx lobes basally toothed ..... 3. *S. maxonis*

1. **Siphocampylus albiguttur** McVaugh, N. Amer. Fl. 32A: 109. 1942. TYPE: Panama, *Allen 2237* (US, holotype, MO, US, isotypes).

Suffrutescent *herbs* 40–70 cm tall; stems glabrous. Median *leaves* with blades stiff and somewhat leathery, at least when dry, ovate, apically acute to vaguely acuminate, basally rounded, rarely subcordate or slightly tapering, glabrous on both surfaces, marginally serrate with 6–8 sharp to rounded, callose, often purple teeth per cm, mostly 4–7 cm long, (2.0–)3.0–4.8 cm wide, usually about twice as long as wide; petioles 1–2(–3.5) cm long, glabrous. *Flowers* ca. 4 cm long; pedicels solitary in the axils of the upper leaves, sparingly to moderately spreading short-pubescent, the hyaline trichomes 0.2–0.4 mm long; bracteoles 2, basal or submedial, filiform, usually 3–6 cm long; hypanthium obconic, spreading short-pubescent with trichomes 0.2–0.4 mm long; calyx lobes oblong, entire, ciliate, 4–5.5 mm long; corolla externally moderately to densely, spreading short-pubescent with trichomes 0.2–0.5 mm long, internally glabrous, the tube dark pink except for the distal 1.5–3 mm white border, 23–27 mm long, fenestrate, the basal 6–8 mm cylindric and 2–3 mm in diameter, expanding above to 5–7 mm in diameter, the lobes white, lanceolate or narrowly triangular, long-tapering, the 2 upper lobes 7–9 mm long, the 3 lower lobes slightly shorter; filament tube 30–32

mm long, glabrous, the filaments distinct and adnate to the corolla for about ⅓ their length, the anthers 3–4.5 mm long, the 2 shorter anthers ca. 3 mm long and apically white-tufted with a dense brush of white trichomes ca. 1 mm long, the 3 other anthers glabrous or sparingly pubescent externally. *Capsules* about half inferior, ellipsoid, ca. 8.5 mm long; seeds oval, dark brown, slightly flattened, shallowly pitted.

Siphocampylus albiguttur is known only from the type collection made in 1940.

COCLÉ: Hills N of El Valle de Antón, 800 m, *Allen 2237* (MO, US).

2. **Siphocampylus darienensis** Wilbur.[16] TYPE: Panama, *Gentry & Mori 13931* (DUKE, holotype; MO, isotype).

Slender perennial *herbs* (?) or *shrublets* ca. 50 cm tall; brachlets terete, spreading short-pubescent, ca. 2.5 mm in diameter. Principal *leaves* with blades thinly membranous when dry, 11–13 cm long, (2–)3–4 cm wide, usually about 3–4 times as long as wide, lanceolate, apically long-acuminate, basally rounded, inconspicuously appressed short-pubescent above and beneath or with spreading trichomes 0.2–0.4 mm long on the principal veins, marginally inconspicuously serrulate with pale yellowish callosities 2–5 mm apart; petioles spreading short-pubescent, 5–9 mm long. *Flowers* 33–38 mm long, borne in loose terminal racemes, the axis ca. 4 cm long; pedicels ebracteolate, stiffly spreading, 3.5–4.5 cm long, 0.5 mm in diameter, clearly articulated 1–4 mm from the base; hypanthium 5–9 mm long, obconic at anthesis, glabrous to sparsely spiculate, conspicuously longitudinally nerved; calyx lobes narrowly linear-lanceolate, 4–6 mm long, ca. 0.8 mm wide at the base, entire, glabrous, erect; corolla orange and yellow, externally glabrous or sparsely and minutely short-pubescent, the trichomes ca. 0.5 mm long or less, internally glabrous, the tube orange, straight, 22–26 mm long, 7–9 mm in diameter above, the 5–6 mm long base abruptly contracted to ca. 2 mm in diameter; the lobes yellowish, all erect and straight, the 2 upper lobes 4–6 mm long, the 3 lower lobes 5–8 mm long; filament tube 23–28 mm long, about as long as the corolla tube, the anther tube 3.5–4.5 mm long, externally abundantly villous with pale lavender trichomes 0.8–1.0 mm long. *Capsules* ⅘ inferior or more, 9–12 mm long; seeds plump, reddish brown, shallowly pitted, ca. 0.5 mm long.

This species is known only from the type collection.

DARIÉN: Cerro Tacarcuna, S slope, ridge top forest well below summit, premontane wet forest, 1250–1450 m, *Gentry & Mori 13931* (DUKE, MO).

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[16] *Siphocampylus darienensis* Wilbur, sp. nov. Herba perenne vel suffrutex; ramuli pubescens. Lamina foliorum lanceolata, serrulata, 11–13 cm longa et (2–)3–4 cm lata, 3–4-plo longiora quam lata, basi rotundata, ad apicem acuminata, supra et subtus sparse strigillosa; petioli pubescens, 5–9 mm longi. Inflorescentia racemosi terminali. Flores ca. 33–38 mm longi; pedicelli ebracteolati, 3.5–4.5 cm longi. Hypanthium obconicum, 5–9 mm longum, glabratum; lobi calycis lineari-lanceolati, 4–6 mm longi, integri, glabri, erecti. Corolla aurantiaca et lutea, glabrata; tubus 22–26 mm longa et supra ca. 7–9 mm diametro et subtus ca. 2 mm diametro; lobi 4–8 mm longi, erecti. Filamenta 23–28 mm longa; tubus anthearum 3.5–4.5 mm longus, villosus. Capsula 9–12 mm longa.

3. **Siphocampylus maxonis** F. E. Wimmer, Repert. Spec. Nov. Regni Veg. 19: 259. 1924. TYPE: Panama, *Maxon 5433* (US, lectotype).—FIG. 7.

Straggly, little-branched, suffrutescent *herbs* or slender *shrublets* 30–60(–100) cm tall; stems glabrous below and throughout most of the length, sparsely to moderately pubescent above with soft, spreading hairs. Medium *leaves* with blades thinly membranous when dry, ovate to lance-ovate, apically long-acuminate, basally cordate, (4–)6–10 cm long, 2.5–5 cm wide, usually 2–2.5 times as long as wide, glabrous above and sparsely short-pubescent on the principal veins beneath, the hyaline trichomes spreading at right angles from the veins and paralleling the surface, marginally sharply serrate to somewhat dentate, the teeth callose-tipped and 0.2–0.4 mm long; petioles sparingly spreading short-pubescent, 1.5–4 cm long. *Flowers* solitary in the axils of the upper leaves, 3.8–4.5 cm long; pedicels solitary, sparsely spreading short-pubescent, 3–4.5 cm long; bracteoles basal, filiform, 2 or lacking, hypanthium obconic or turbinate at anthesis, moderately to densely spreading short-pubescent with hyaline trichomes 0.2–0.5 mm long; calyx lobes narrowly linear, subulate, the pubescence mostly restricted to marginal cilia and along the midvein, 4–7 mm long with 2–4 slender marginal, appressed, basal teeth; corolla red or rose purple, externally sparsely to moderately spreading short-pubescent, the trichomes 0.1–0.2 mm long, internally glabrous, the tube straight, 25–30 mm long, the base 6–8 mm long, narrowly cylindric, 1.5–2 mm in diameter, the upper portion expanding to 4–7 mm in diameter, the 2 upper lobes 8–12 mm long, the 3 lower lobes 7–9 mm long; filament tube 30–34 mm long, glabrous, slightly exserted, slightly adherent to the base of the corolla, the anther tube 4–5 mm long, the 2 shorter anthers apically white-tufted with trichomes ca. 1 mm long, the other anthers glabrous or with a few scattered trichomes or a line of hairs in the commissures. *Capsules* ca. ⅔–¾ inferior, ca. 8 mm long; seeds plumply cylindric to subglobose, shallowly pitted with isodiametric depressions, 0.5–0.7 mm long.

Siphocampylus maxonis is known only from Chiriquí Province on the southern slope of Cerro Horqueta, where it is locally so abundant as to appear almost weedy.

CHIRIQUÍ: S flank of Cerro Horqueta, 1750–2100 m, *Cochrane et al. 6281* (MO). S slopes of Cerro de la Horqueta, Las Siguas Camp, 1700 m, *Maxon 5433* (US). Cuesta de Las Palmas, S slope of Cerro de la Horqueta, 1700–2100 m, *Pittier 3157* (US). Los Siguas Camp, Cuesta de Las Palmas, S slope of Cerro de la Horqueta, 1700–2100 m, *Pittier 3209* (NY, US). S slopes of Cerro Horqueta, N of Boquete, ca. 6000 ft, *Wilbur et al. 13463* (DUKE, F, GH, LL, MICH, MO, NY, PMA, US, WIS). Ca. 6.6 km NNE of Boquete, 1500–1800 m, *Wilbur & Luteyn 19262* (BM, BR, CAS, CR, DUKE, F, FSU, G, GH, HAL, K, LL, MICH, MO, MSU, NY, P, PMA, SU, UC, US, USF, W, WIS), *19290* (DUKE, MICH).

7. SPHENOCLEA

Sphenoclea Gaertn., Fruct. Sem. Pl. 1: 113, *pl. 24, fig. 5.* 1788, nom. cons. TYPE: S. *zeylanica* Gaertn.

Pongati Adanson, Hist. Nat. Senegal 83. 1757.
Pongatium Juss., Gen. Pl. 423. 1789.
Rapinia Loureiro, Fl. Cochinch. 1: 127. 1790. TYPE: *R. herbacea* Loureiro.
Gaertnera Retz., Obs. Bot. 6: 24. 1791. TYPE: *G. pangati* Retz.

FIGURE 7. *Siphocampylus maxonis* F. E. Wimmer.—A. Habit (×⅘).—B. Filament tube, anther tube, and exserted style (×4⅗). [After *Wilbur & Luteyn 19262* (DUKE).]

Annual *herbs*; stems spongy, glabrous, fistulous. *Leaves* entire, simple, exstipulate, alternate, shortly petiolate, pinnately veined. *Inflorescences* dense, terminal, pedunculate spikes. *Flowers* sessile, each subtended by a bract and a pair of bracteoles; hypanthium laterally compressed; calyx lobes triangular to suborbicular, usually slightly wider than long; corolla white with imbricate lobes, deciduous soon after anthesis; stamens 5, the filaments very short, alternating with the corolla lobes and borne on the corolla tube near its middle or slightly below, the anthers rounded, appearing peltate, dehiscing longitudinally; style erect, terminated by a capitate stigma, the ovary completely inferior. *Capsules* bilocular, circumscissilely dehiscent, with a conspicuous axile placentae; seeds oblong-cylindric with 10–12 narrow ridges, shallowly and indistinctly pitted in the areas between the longitudinal ridges.

This is a monotypic genus native to the Old World Tropics but frequently introduced into weedy, moist habitats in the tropics and subtropics of the New World.

Airy Shaw (1948) argued that this genus ought to be recognized as the monogeneric family Sphenocleaceae and provisionally positioned as a "half-way house" between the Phytolaccaceae and the Primulaceae. Most phylogenists, however, treat *Sphenoclea* as a member of the Campanulaceae s. lat. or of a closely related segregate family.

Literature:

Airy Shaw, H. K. 1948. Sphenocleaceae. *In* C.G.G.J. van Steenis (editor), Flora Malesiana 4: 27–28.

1. **Sphenoclea zeylanica** Gaertn., Fruct. Sem. Pl. 1: 113, *pl. 24, fig. 5.* 1788. TYPE: not seen.—FIG. 8.

Rapinia herbacea Loureiro, Fl. Cochinch. 1: 127. 1790. TYPE: not seen.
Gaertnera pangati Retz., Obs. Bot. 6: 24. 1791. TYPE: not seen.
Pongatium indicum Lam., Tabl. Encycl. Méth. 1: 444. 1793. TYPE: not seen.
Sphenoclea pongatium DC., Prodr. 7: 548. 1839. TYPE: not seen.
Pongatium zeylanicum (Gaertn.) Kuntze, Rev. Gen. Pl. 2: 381. 1891.

Annual *herbs*; stems glabrous, spongy, 0.5–1.0(–1.3) m tall, usually hollow and widely branched above. *Leaf blades* entire, ovate to elliptic, mostly 6–12 cm long, 2–3.5(–6) cm wide, obtuse to acute and bluntly mucronate apically, cuneately tapering basally, glabrous; petioles mostly 0.5–2.0 cm long, glabrous. *Spikes* densely congested with as many as 100 flowers per cluster, cylindric, usually 2.5–8 cm long and 6–9 mm in diameter, terminating the main stems and axes; peduncles 1.5–5(–10) cm long. *Flowers* sessile, subtended by spatulate bracts with acute to acuminate apices, 2–3 mm long; bracteoles paired, linear, erose-tipped, 2–3 mm long; hypanthium laterally compressed, basally broadly fused to the axis of the spike, thinly cartilaginous at maturity; calyx lobes broadly and bluntly deltoid to suborbicular, 1.5–2.5 mm long, slightly less in width, apically rounded and both erose and scariously tipped, inflexed and partially covering the apex of the capsule at maturity; corolla white, ca. 2.5 mm long, the tube 1–1.5

FIGURE 8. *Sphenoclea zeylanica* Gaertn.—A. Habit (×⅘).—B. Fruit (×15⅖). [After *Busey* 579 (DUKE).]

mm long, the lobes imbricate, triangular, blunt, 1.0–1.2 mm long; filaments filiform, ca. 0.4 mm long, borne at or just below the middle of the corolla tube, the anthers ca. 0.5 mm long. *Capsules* circumscissilely dehiscent, 2.5–3.0 mm high, 3–4 mm in diameter; seeds pale yellowish brown, ca. 0.5 mm long, oblong-cylindric, lustrous, longitudinally striate with 10–12 ridges, shallowly and indistinctly pitted between the ridges.

Sphenoclea zeylanica is an introduction from the Old World Tropics and is now widespread in moist weedy habitats through the warmer parts of the Americas, ranging from Louisiana, Arkansas, and Texas southward sporadically at least as far as Paraguay.

BOCAS DEL TORO: Almirante, *Blum 1311* (MO). CANAL ZONE: Victoria Fill, near Miraflores Locks, *Allen 1718* (GH, MO, US). CHIRIQUÍ: Burica Peninsula, 6 km W from airport of Puerto Armuelles, 60–100 m, *Busey 579* (DUKE, MO). Ca. 2 mi S of Puerto Armuelles, *Wilbur et al. 13547* (DUKE, MO).

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THE GENUS *MORAEA* IN THE WINTER RAINFALL REGION OF SOUTHERN AFRICA[1]

PETER GOLDBLATT[2]

ABSTRACT

The genus *Moraea* (Iridaceae), a close relative of *Iris*, and believed to have evolved independently of *Iris* from *Dietes*, is an exclusively African genus. It ranges from Nigeria and Ethiopia south through the African highlands to the southern tip of Africa where a winter rainfall regime prevails. *Moraea* appears to have radiated explosively in this region where 54 of the 93 species are found, 51 essentially being endemic. The winter rainfall region is also the center of diversity of *Moraea* and the probable area of origin for the genus. The present revision, the first since Baker's (1892) treatment in *Flora Capensis*, includes details of phylogeny, ecology, phytogeography and cytology, with new chromosome reports for five species. The treatment includes descriptions of nine new species and one new combination.

Moraea, one of the larger genera of the Iridaceae, is closely related to the well known *Iris* and can be regarded as an African counterpart of this genus. It belongs with *Iris* in subfamily Iridoideae, and in the tribe Irideae, which includes the Old World representatives of this subfamily. It comprises approximately 92 species which are widely distributed in sub-Saharan Africa. Species occur mainly in the more temperate highland areas and the concentration increases considerably towards the south. In South Africa alone there are 74 species. Of this number, 54 occur in the southern African winter rainfall region which embraces the southern and western part of the Cape Province of South Africa as well as the extreme southern portion of South West Africa (Namibia), where a single species only is found.

[1] I wish to thank Professor T. T. Barnard, Compton Herbarium, Kirstenbosch, South Africa for sharing his knowledge of *Moraea* gained over many years and particularly for his generous advice with historical data. I also thank my wife, Margaret, for her invaluable assistance in the field, in the drawing of the maps, and in the preparation of the manuscript. Illustrations by Margo Branch are gratefully acknowledged. Support for this study was provided by a grant from the U.S. National Science Foundation (BMS-74-18905) from 1974 to 1976 and from the South African Council for Scientific and Industrial Research in 1971.

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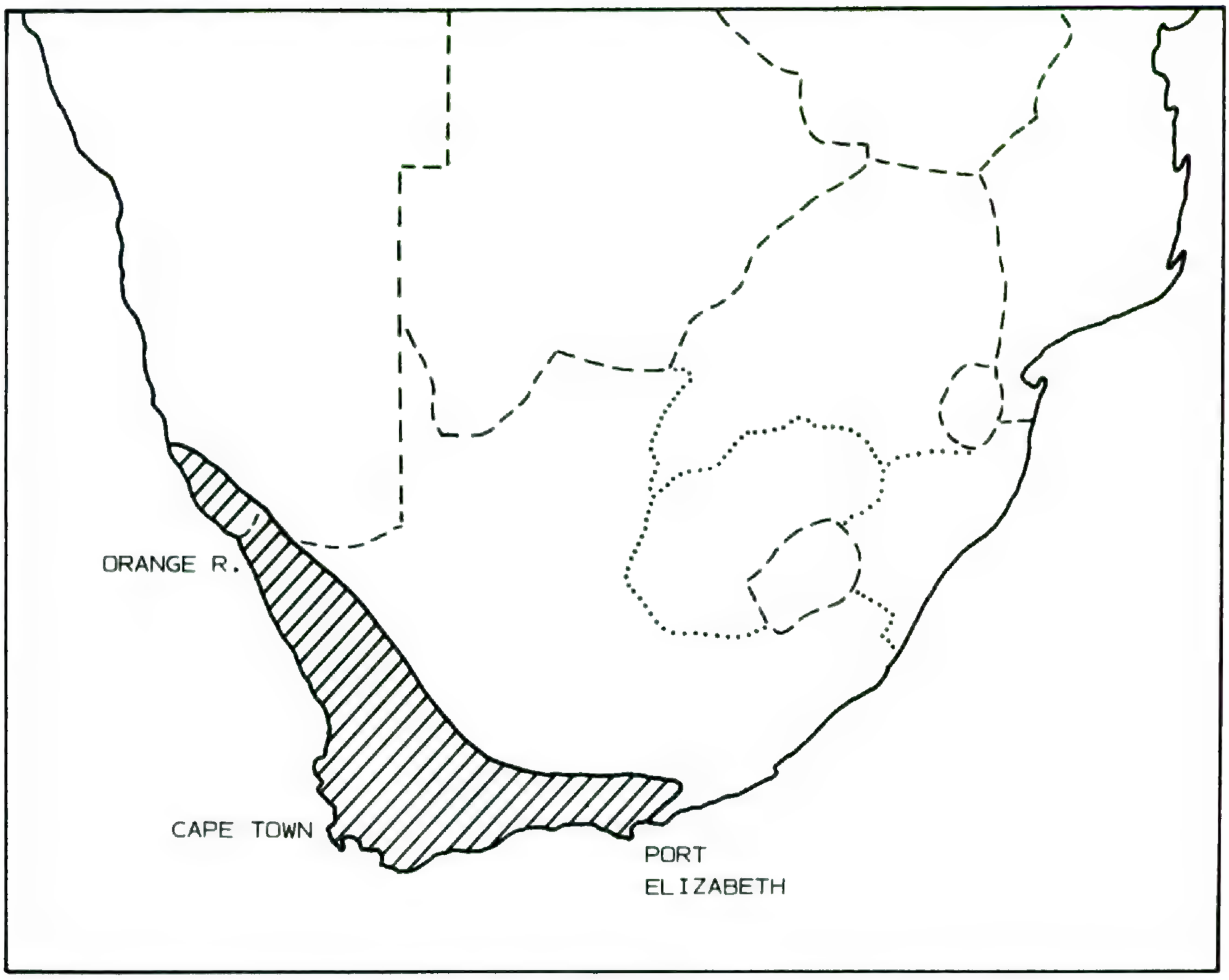

FIGURE 1. Southern Africa with the winter rainfall region shaded.

The genus is currently being revised in three stages. A treatment of the species of the summer rainfall region of southern Africa (South Africa, Botswana, Lesotho, Swaziland, and South West Africa) has been published (Goldblatt, 1973), and the present paper constitutes the second phase embracing the southern African winter rainfall region. A study of the tropical African species, already in progress, will form the final part of the revision. Cytological studies undertaken in conjunction with the taxonomic work has led to a considerably clearer understanding of the evolution and relationships of species within the genus. Cytology has been particularly significant at the subgeneric level where different basic chromosome numbers and varied karyotypes have provided the rationale for a redefinition of subgenera and sections, and has formed the basis for a revised subgeneric classification (Goldblatt, 1976a).

The winter rainfall region as delineated here forms a natural phytogeographic zone and *Moraea* exhibits a high degree of endemism within the area. Of the 54 species found here, two, *M. spathulata* and *M. polystachya*, are summer rainfall region species with minor range extensions into the winter rainfall zone, and as such are not dealt with in detail, while a third, *M. falcifolia* is equally distributed in both rainfall zones. The remaining 51 are essentially endemic in the winter rainfall region with only four species having a limited extension into adjacent parts of the summer rainfall zone.

Geographic Limits: The Winter Rainfall Zone of Southern Africa

The winter rainfall area of southern Africa, with a climate unlike that of the rest of sub-Saharan Africa, has a very characteristic and rich flora, and a large part of this area is often regarded as one of the six major floristic regions of the world (Good, 1968). It is here, in what is generally known as the Cape Floral Region, that *Moraea* has its present center of development. The greatest range of variation in the genus, as well as the majority of species, is found entirely within this area. The actual geographic limits of the Cape Floral Region are not clearly defined, but usually include the southern Cape coast from Port Elizabeth to Cape Town, extending north to embrace the Cedarberg and Nieuwoudtville area some 300 km to the north. The winter rainfall region as treated here includes not only this area, but the area to the north generally known as Namaqualand, as well as the extreme southwestern tip of South West Africa (Fig. 1). The region thus defined receives predominantly winter rainfall and forms a phytogeographic unit as far as *Moraea* is concerned. The area included in this treatment receives at least 40% and up to 100% of its rainfall in the winter months between May and October (Adamson, 1938). By this definition the area west of a line drawn from Port Elizabeth and Grahamstown in the east, to Laingsburg and then to Luderitz Bay, South West Africa, in the northwest is regarded here as the winter rainfall region of southern Africa (Fig. 1), complementing the summer rainfall region as defined earlier by me (Goldblatt, 1973).

Relationships of *Moraea*

ORIGIN AND ANCESTRY

Moraea is a member of subfamily Iridoideae, tribe Irideae, and is related to the Old World representatives of this tribe (Table 1). It is closely allied to the widespread northern hemisphere genus *Iris*, and probably shares with it a common origin in *Dietes*, perhaps the most primitive genus of Irideae, or the immediate ancestors of this genus (Goldblatt, 1976a). The characteristic features of these three genera are the *Iris*-like flower with large spreading outer tepals, small inner tepals, and petaloid style branchs with large paired crests. *Dietes* has a woody, rhizomatous rootstock, evergreen typically Iridaceous equitant leaves, and free tepals and stamens. *Iris*, with either a rhizomatous or bulbous rootstock, is specialized in being predominantly deciduous, and in having tepals united in a tube.

Moraea differs from both in its distinctive cormous rootstock, bifacial leaves, deciduous habit, and though the tepals are free in all but two species, the stamens are usually partly united. As discussed in a previous paper, these modifications are predominantly adaptations to a dry seasonal climate with only a short growing season (Goldblatt, 1976a).

GENERIC LIMITS AND AFFINITIES

Moraea is clearly distinct from the northern hemisphere *Iris* as well as from the less specialized and presumably ancestral *Dietes*, though this genus has often

been included in *Moraea*. *Dietes* in fact has more in common with *Iris* and is certainly best regarded as a distinct genus, ancestral to both *Moraea* and *Iris*, as suggested by Salisbury (1812) and Spae (1846) and recently supported by myself (Goldblatt, 1971, 1976a). *Moraea* is less distinct, however, from several small and closely related genera including *Homeria*, *Hexaglottis*, *Gynandriris*, the recently recognized *Barnardiella* (Goldblatt, 1976b), and also *Galaxia* (though this is perhaps more sharply defined than the others). All share with *Moraea* a characteristic corm and corm tunic, a basically bifacial to occasionally terete leaf, deciduous habit, and similar inflorescence structure; because of these similarities, all except *Galaxia* have at one time been included in *Moraea*.

Homeria, with subequal tepals and the style branches and style crests much reduced or with the crests lacking, differs least. It may conceivably even be polyphyletic, including more than one evolutionary line from *Moraea* with reduced style crests. *Hexaglottis* represents a further step in the reduction of the style branches, which in this genus are each deeply forked and filiform.

Gynandriris is perhaps equally closely related to *Moraea*. It has flowers like species such as *M. polyanthos*, but is easily distinguished by the peculiar sterile prolongation of the ovary which forms a tube, raising the flower above the inflorescence spathes. This tube, together with distinctive transparent spathes, make this small genus easy to recognize. *Gynandriris* has in the past frequently been included in *Moraea* as subgenus *Helixyra*. It has also been included in *Iris* which quite wrongly reflects its natural relationships (unless *Moraea* too is included in *Iris*). The decision finally to regard *Gynandriris* as distinct was made by Brown (1929), and except for the inclusion of *G. sisyrinchium* in *Iris* by various European botanists, this decision has generally been followed.

The recently described *Barnardiella* is peculiar in two respects: it has an ovary tube like that found in *Gynandriris*, while its flower is similar to that of *Homeria*, with reduced style branches and crests. Cytological evidence (Goldblatt, 1976b) suggests an independent origin from *Moraea* subgenus *Moraea*.

As already mentioned, *Galaxia* is a more clearly defined genus than the other close relatives of *Moraea*. A flower with a long perianth tube, and a stemless habit, make it distinctive. Its ancestors were probably similar to species such as *Moraea falcifolia* (*Moraea* subgenus *Moraea*) from which it differs mainly in having a perianth tube and reduced style crests.

It is fairly obvious that *Homeria*, *Hexaglottis*, *Gynandriris*, and *Barnardiella* are all very closely related to *Moraea*. However, they appear to the present author to merit generic status, not only because each constitutes a natural group, but also since any enlargement of *Moraea* would make this genus, already comprising five subgenera, unwieldy. In an earlier classification (Goldblatt, 1971) I had included *Moraea* with *Gynandriris*, *Dietes* and *Iris* in Iridinae while regarding *Homeria*, *Hexaglottis*, and *Galaxia* as constituting a separate subtribe, Homeriinae. However, it now seems preferable to include all the cormiferous, bifacial-leafed members of Iridoideae-Irideae in a single alliance (Table 1); the earliest name for such a group being Homeriinae (Goldblatt, 1971). *Dietes*, together with *Iris* and its segregates with either rhizomatous or bulbous rootstocks

TABLE 1. Classification of the African Iridoideae tribe Irideae.

Subtribe 1. *Iridinae*
Iris (s.l.), *Hermodactylis*, *Belamcanda*, *Dietes*.

Subtribe 2. *Homeriinae* Goldbl.
Moraea, *Homeria*, *Hexaglottis*, *Gynandriris*, *Barnardiella*, *Galaxia*.

Subtribe 3. *Ferrariinae* Goldbl.
Ferraria.

then constitute the Iridinae. The only other African member of the Iridoideae-Irideae, *Ferraria*, seems well placed in its own subtribe, Ferrariinae as suggested earlier by me (Table 1).

DELIMITATION OF SUBGENERA AND SECTIONS

In order to assist the reader in understanding the introductory discussion that follows, the subgenera, sections, and species are presented in outline in Table 2. Species of subgenus *Vieusseuxia* and *Grandiflora* occurring outside the winter rainfall region are not listed.

As a result of data now known, the subgeneric classification proposed by Baker (1896) has been considerably modified (Goldblatt, 1976a). Five subgenera are recognized, three of which, *Moraea*, *Visciramosa* and *Monocephalae*, are regarded as having evolved along independent paths from an ancestral stock. Each has retained the postulated basic chromosome number for the genus, $x = 10$, and usually has an unspecialized morphology. The presumably primitive and ancestral features of multiple branching, two to several leaves, and simple flower structure occur in subgenus *Visciramosa* and some species of subgenus *Moraea*. Subgenus *Monocephalae* as well as certain members of subgenus *Moraea* are, however, vegetatively specialized with a single leaf and reduced branching.

The two remaining subgenera, *Vieusseuxia* and *Grandiflora* have a derived base number, $x = 6$, and are variously modified. In subgenus *Vieusseuxia* floral specialization predominates, and all except three or four species are unifoliate. Species of subgenus *Grandiflora* are large, single leafed, invariably unbranched, and, although the flowers themselves are unspecialized, the flat discoid seeds are characteristic. Similar seeds are also found in subgenus *Monocephalae*; the two subgenera are, however, considered to be unrelated.

Subgeneric delimitation has been largely based on cytological data and the resulting divisions clearly comprise natural assemblages. Morphologically, however, there is often little to distinguish the single-leafed, fewer-branched species of subgenus *Moraea* (section *Deserticola*) from the florally unmodified members of subgenus *Vieusseuxia* (section *Polyanthes*), nor the few multi-leafed members of *Vieusseuxia* from those of subgenus *Moraea*. The less robust and small-flowered species of subgenus *Grandiflora* are almost equally difficult to distinguish from subgenus *Vieusseuxia* in the absence of seeds, which of course are seldom collected. For such reasons a key to the subgenera is impractical and is not provided.

Sections are recognized only in subgenera *Moraea* and *Vieusseuxia*, and are

TABLE 2. Subgenera, sections, and species of *Moraea*.

I. Subgenus *Moraea*

Section 1. *Moraea*

1. *M. ramosissima* (L.f.) Druce
2. *M. gawleri* Spreng.
3. *M. vegeta* L.
4. *M. indecora* Goldbl.
5. *M. fergusoniae* L. Bol.
6. *M. papilionacae* (L.f.) Ker
7. *M. margaretae* Goldbl.
8. *M. serpentina* Baker
9. *M. tortilis* Goldbl.
10. *M. lugubris* (Salisb.) Goldbl.

Section 2. *Acaules*

11. *M. falcifolia* Klatt
12. *M. ciliata* (L.f.) Ker
13. *M. macronyx* Lewis
14. *M. tricolor* Andrews

Section 3. *Deserticola*

15. *M. saxicola* Goldbl.
16. *M. macgregorii* Goldbl.
17. *M. namibensis* Goldbl.
18. *M. bolusii* Baker

Section 4. *Subracemosae*

19. *M. gracilenta* Goldbl.
20. *M. fugax* (de la Roche) Jacq.

Section 5. *Tubiflora*

21. *M. cooperi* Baker
22. *M. longiflora* Ker

II. Subgenus *Visciramosa*

23. *M. bituminosa* (L.f.) Ker
24. *M. bubalina* Goldbl.
25. *M. viscaria* (L.f.) Ker
26. *M. inconspicua* Goldbl.
27. *M. elsiae* Goldbl.

III. Subgenus *Monocephalae*

28. *M. angusta* (Thunb.) Ker
29. *M. anomala* Lewis
30. *M. neglecta* Lewis

IV. Subgenus *Vieusseuxia*

Section 6. *Polyanthes*

31. *M. polystachya* (L.f.) Ker
32. *M. polyanthos* Thunb.
33. *M. nubigena* Goldbl.

Section 7. *Vieusseuxia*

34. *M. algoensis* Goldbl.
35. *M. tripetala* (L.f.) Ker
36. *M. debilis* Goldbl.
37. *M. barnardii* L. Bol.
38. *M. incurva* Lewis
39. *M. barkerae* Goldbl.
40. *M. thomasiae* Goldbl.
41. *M. unguiculata* Ker
42. *M. lurida* Ker
43. *M. insolens* Goldbl.
44. *M. tricuspidata* (L.f.) Lewis
45. *M. bellendenii* (Sweet) N.E.Br.
46. *M. neopavonia* Foster
47. *M. gigandra* L. Bol.
48. *M. caeca* Barnard ex Goldbl.
49. *M. aristata* (de la Roche) Asch. & Graeb.
50. *M. amissa* Goldbl.
51. *M. villosa* (Ker) Ker
52. *M. tulbaghensis* L. Bol.
53. *M. loubseri* Goldbl.

V. Subgenus *Grandiflora*

54. *M. spathulata* (L.f.) Klatt

based entirely upon morphological considerations. Differences between sections are sharp, being based on gross features. In subgenus *Moraea*, the entirely subterranean stem distinguishes section *Acaules*; a perianth tube, section *Tubiflora*; a beaked ovary and lack of basal leaf, section *Subracemosae*; and a solitary leaf

and dark corm tunics, section *Deserticola*. Floral differences distinguish the two sections of subgenus *Vieusseuxia*, with flowers of the specialized section *Vieusseuxia* differing from those of section *Polyanthes* in their modified and reduced inner tepals. Unlike the divisions between the subgenera, these sectional differences are not reflected in the cytology, and their karyotypes do not differ markedly. Morphological similarities between the sections make their relationships fairly clear and sectional affinities are discussed in the taxonomic treatment.

Cytology

Chromosomal characteristics have proved of considerable value in the understanding of evolution and phylogeny in *Moraea*, providing the basis for the recent subgeneric classification (Goldblatt, 1976a). With the counts for five newly described species reported here for the first time,[3] chromosome number is known for 55 species, almost 60% of the genus. The pattern which has emerged has been fully described elsewhere and is only briefly summarized below. Documentation of chromosome numbers listed for each species has been presented in an earlier paper (Goldblatt, 1976a) and is not repeated here.

The base number for the genus is probably $x = 10$, the same as that in *Dietes*. In the three subgenera regarded as primitive, *Moraea*, *Visciramosa*, and *Monocephalae*, $x = 10$ is clearly basic, though gametic numbers of $n = 9, 8, 6$ also occur in the large subgenus *Moraea*. The two specialized and independently derived subgenera, *Vieusseuxia* and *Grandiflora*, have a base number of $x = 6$, and only multiples based on $x = 6$ occur in these subgenera.

The chromosomes of *Moraea* are large, and a variety of karyotypes has provided many indications of the relationships of species and sections. As karyotypic details have already been fully described, they are only mentioned in the taxonomic treatment when particularly relevant to the generic and sectional relationships or when significant in understanding the status or evolution of certain species.

Geography

For the purpose of this discussion, the winter rainfall area has been divided into three clearly defined divisions found to be significant in the distribution of *Moraea* (Fig. 2). The detailed phytogeographic units described by Weimarck (1941) for the Cape Floral Region are not considered, as *Moraea*, with its range extending well to the north of the area treated by Weimarck, is by no means a typical member of the Cape Flora.

A total of 54 species of *Moraea* occur in the winter rainfall region, and the majority, 47 species, are endemic. Of the seven species which extend beyond the limits of the region (Fig. 1) two, *Moraea spathulata* and *M. polystachya*, may be considered summer rainfall region species with minor extensions of their range

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[3] Chromosome counts for the following species are reported here for the first time: *Moraea indecora*, *M. tortilis*, *M. saxicola*, *M. macgregorii*, and *M. barkerae*. Voucher information for these counts is given following the species descriptions.

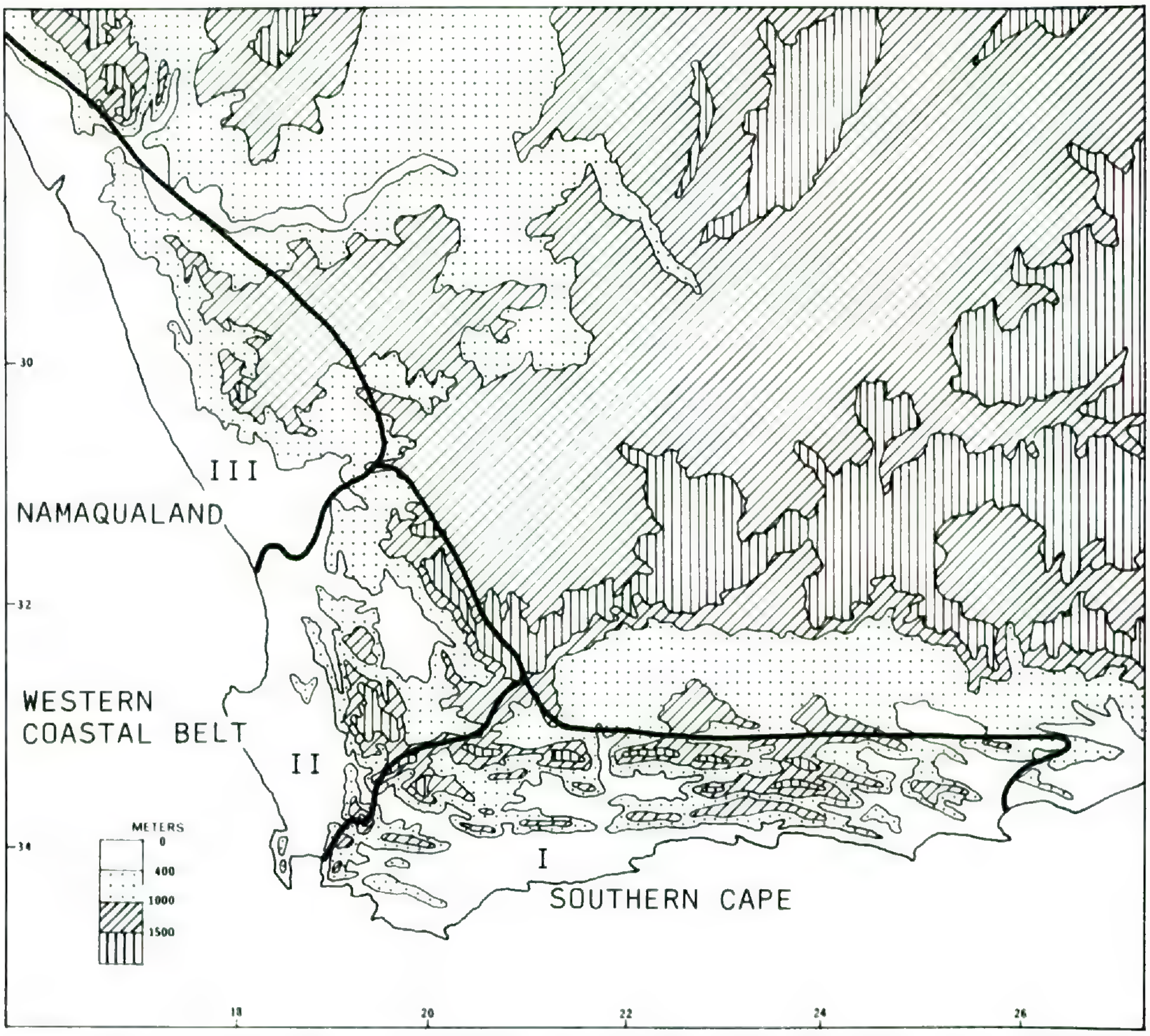

FIGURE 2. The three phytogeographic regions into which the winter rainfall region has been divided here.—I. Southern Cape.—II. Western Coastal Belt.—III. Namaqualand.

into the winter rainfall region. The remainder, *Moraea polyanthos*, *M. serpentina*, *M. ciliata*, and *M. unguiculata*, have very minor range extensions into the summer rainfall zone, while *M. falcifolia* is equally distributed over both summer and winter rainfall portions of the Cape Province. The majority of species of *Moraea* occur in only one or two of the three phytogeographic divisions of the winter rainfall region recognized here, and only five species occur over almost the entire area, these being *M. gawleri*, *M. fugax*, *M. inconspicua*, *M. unguiculata*, and *M. ciliata*, the last two also extending into the summer rainfall region. Following are the three phytogeographic divisions:

I. The Southern Cape, including the Little Karoo and Long Kloof: This area extends from Grahamstown and Port Elizabeth in the east to the Hottentots Holland Mountains in the west. Almost all of this region may receive at least limited, though significant, summer precipitation. (30 species, 8 endemic.)

II. The Western Coastal Belt: This area extends from the Cape Peninsula north to Nieuwoudtville and the mountains of the Van Rhynsdorp district, and reaches inland to include the Warm and Cold Bokkeveld. Except in the extreme south, this region receives almost entirely winter rain. (34 species, 11 endemic.)

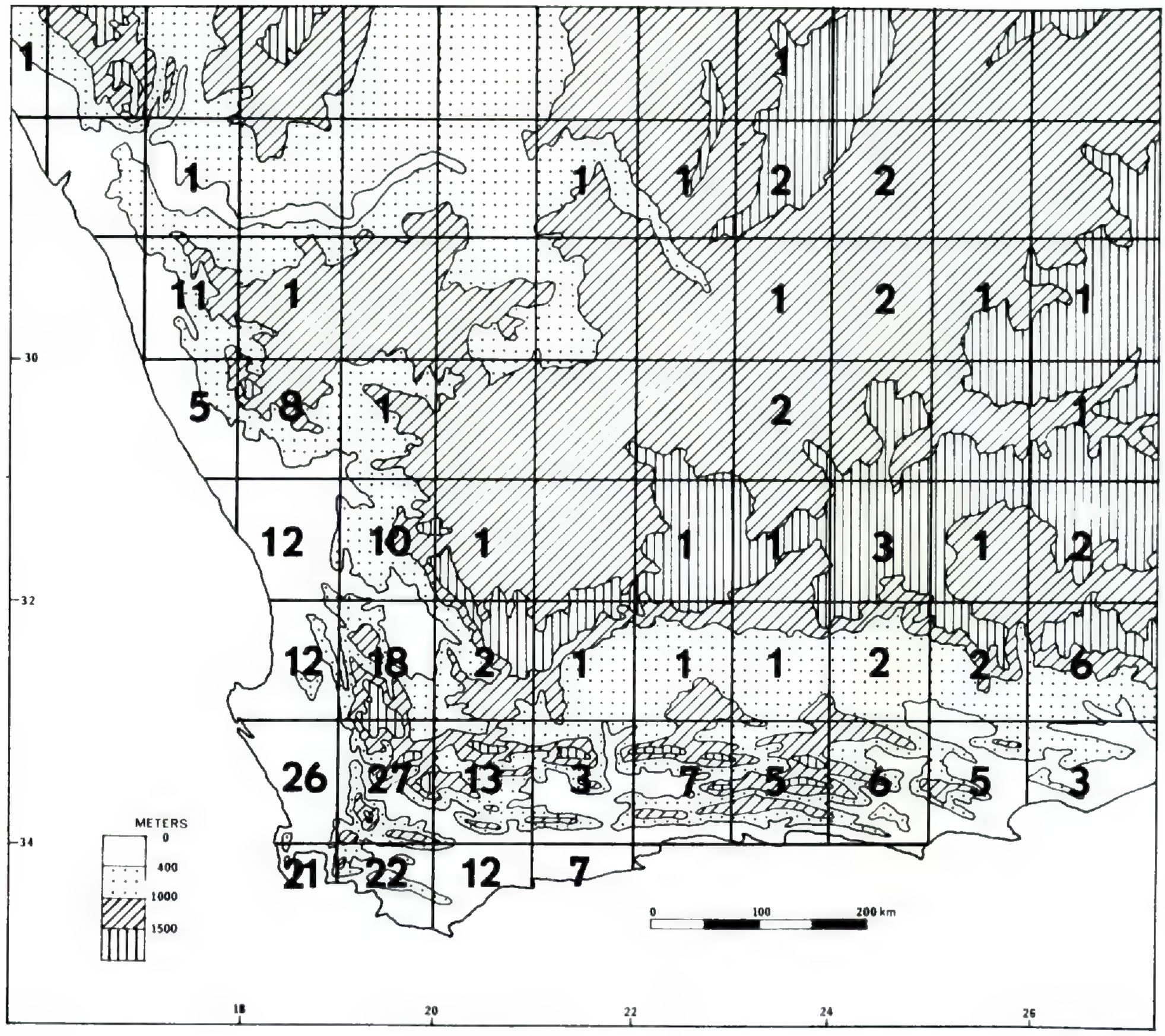

FIGURE 3. Concentration of species of *Moraea* in the southern African winter rainfall region and adjacent areas. Figures indicate the number of species in each geographical degree square.

III. Namaqualand: This area includes the arid northwestern Cape, from the Van Rhynsdorp district northwards, and it extends as far as southern South West Africa. The region is extremely arid, receiving less than 25 cm of annual precipitation, mainly in the winter months. (16 species, 8 endemic.)

If the geographical distribution of *Moraea* in the winter rainfall region is considered in the light of a superimposed grid, the lines of which for convenience are taken as whole number geographical coordinates, the following pattern emerges. The greatest number of species of *Moraea* are found in the extreme southwestern part of the region, and the concentration decreases to the east and to the north (Fig. 3), a pattern typical of species occurring in the Cape Flora (Dahlgren, 1963). There are 26 species in the Cape Town grid (33.18)[4]

[4] Plant distributions in southern Africa are often expressed in terms of geographical degree squares rather than by administerial districts. Each square or grid is defined by a degree of latitude and longitude and is expressed in numerical terms as well as by the name of a major town within it (Edwards & Leistner, 1971).

and 27 in the Worcester grid (33.19) with 3 endemic in the first and 2 in the second. The next highest number of species occurs in the Caledon grid (34.19) where there are 22 species and 3 endemics.

A noteworthy secondary center of species concentration is the Springbok area of Namaqualand (29.17), where 11 species occur, only 1 of which is endemic. This small area is at a fairly high altitude, where cooler temperatures make the prevailing low precipitation particularly effective. In addition, a greater variety of soil types than found elsewhere in Namaqualand provides a correspondingly wider range of available habitats (see discussion under *Moraea saxicola*). The Springbok area is the center of the small section *Deserticola* with two of the four species in the alliance found here.

This secondary Namaqualand center of speciation is known for several genera that are concentrated in the Cape Flora but tolerate the drier situations that surround the region, e.g., *Lapeirousia* (Goldblatt, 1972a) and *Euryops* (Nordenstam, 1969).

With the exception of subgenus *Grandiflora*, only one species of which occurs partly in the winter rainfall region, the four remaining subgenera of *Moraea* are all centered here where subgenera *Moraea*, *Visciramosa* and *Monocephalae* are endemic. These four subgenera and all sections except section *Deserticola* and section *Polyanthes* have their center of distribution in the extreme southwestern Cape. Section *Deserticola* is centered in the Namaqualand region, while section *Polyanthes* has its center in the highlands of southeastern Africa. With the greatest number of species, and with the least specialized subgenera concentrated in the winter rainfall region, it is difficult not to envisage the southwestern Cape as the place of origin of *Moraea*. The fact that the winter rainfall climate is probably a very recent phenomenon, perhaps of the last two million years (Raven, 1973; Axelrod, 1973) tempers this conclusion since the genus must be of considerably greater age. However, *Moraea* probably did evolve in, or somewhat north of, this region, although under a rather different climatic regime, characterized by low, but not winter, rainfall and considerable seasonal aridity (Goldblatt, 1976a).

ECOLOGY

HABITAT

There are three main soil types in the Cape winter rainfall region: clay soils derived from shale; a very characteristic white sandy soil derived from sandstones of the Cape System; and a granite-derived, coarse gritty soil, very common in Namaqualand, and local elsewhere. In areas of high rainfall in the south, the granitic soils tend to become clayey, but in the dry areas to the north, they are well drained and coarse grained. Soil differences are enhanced by the fact that in the rugged topography of the southwestern Cape the mountains are primarily composed of resistant sandstone and the valleys and plains of shales; thus lowland species are mainly found in clay soils and montane species in sandy or stony ground. In fact the range of many species is closely related to soil type and the

southwestern Cape species can generally be classed as lowland and clay, or montane and sand-loving species (Dahlgren, 1968).

In the areas of highest rainfall in the extreme south and west, however, soil type seems less important, and the correlation between species and soil type often breaks down, a pattern in keeping with observations (Raven, 1964) that soil conditions are increasingly critical to plant species in drier climates as rocks weather more slowly so that their chemical constitution becomes more significant. Thus *M. gawleri*, a clay-loving species of slopes and flats in dry areas, may be found on sandy soils in the south, and similarly, *M. unguiculata*, always found on clay in arid areas also occurs on sand in the mountains of the south. In contrast, *M. ciliata*, typically though not invariably sand-loving in drier areas, often occurs on a clay substrate in the Cape and Caledon districts. *Moraea tripetala* is particularly exceptional in that it is found both on sand or clay with equal frequency and appears to comprise several local races each with different ranges and habitats. Most species, however, are readily characterized by a particular soil preference.

Most species of *Moraea* grow in open fynbos, the name given to the small-leafed vegetation of the southwestern Cape, and are not found on wetter slopes and gullies which are often heavily wooded. *Moraea ramosissima* and *M. nubigena* are the only notable exceptions in having an affinity for moist habitats. *Moraea ramosissima* occurs along streams, seepage areas, or forest margins, the latter a situation where *M. spathulata* is also often found. *Moraea nubigena* occupies a unique niche in the genus, growing in moss banks on rock flushes at high altitude. Clay loving species of *Moraea* usually occur in Renosterbos veld (Acocks, 1953), which is a low-growing, fine-leafed scrub, dominated by *Elytropappus rhinocerotis* (L.f.) Less. and other bushy Compositae, and which is particularly rich in geophytic plants of several families. Species growing in the sandy Cape soils share their habitat with more typical fynbos, dominated by sclerophyllous Proteaceae and microphyllous Ericaceae and Rutaceae, and with a ground cover of the characteristic Restionaceae. In many areas the geophytes tend to become crowded out by larger, taller species and may not flower for many years, until the area is cleared artificially or by frequent fires. Some species, such as *M. tricuspidata*, *M. lurida*, and *M. insolens*, are particularly fire responsive and often flower only in the seasons immediately following a burn.

Such habitats as described seldom apply in Namaqualand, where fynbos is barely developed. Species of *Moraea* in this area generally occur in stony places where the corms are sheltered from predators and where additional moisture is available.

FLORAL BIOLOGY

The flowers of many species of *Moraea* are relatively short lived, opening at constant times during the morning or afternoon and lasting until late the same day. In some species they are particularly fugaceous, as in subgenus *Sciramosa* where flowers usually open after midday, about 1:00 P.M. and fade by evening, and one species in the subgenus, *M. viscaria*, opens only after 3:00 P.M.

Short-lived flowers also occur in section *Subracemosae* and section *Deserticola* where blooming takes place during the afternoon. *Moraea macgregorii* and the Cedarberg populations of *M. anomala* (subgenus *Monocephalae*) are especially notable, opening only after 4:00 P.M. and fading shortly after nightfall.

Flowers in section *Vieusseuxia* are generally longer lasting, and in the large-flowered "peacock moraeas," i.e., *Moraea villosa* and its close allies, flowers survive up to three days.

Virtually nothing is known of pollination biology in *Moraea* apart from observations by Scott-Elliot (1891). Many species are heavily and sweetly scented, usually the less brightly colored or marked ones; scent in these is probably an added attractant to the visual stimulus. My experiments on a few species have indicated self-incompatibility: thus species must rely on insect visitors to accomplish pollination. Bees have been observed visiting flowers and are undoubtedly the most important pollinators. The bee normally orients itself by the nectar guide to probe between the outer tepal, claw, and style branch in search of nectar. In doing so it brushes against the receptive upper surface of the stigma, and then only does it come in contact with the anther. Other noted visitors are small day-flying moths and brown skipper butterflies, as well as herbivorous beetles which frequently devour whole flowers when in sufficient number.

Given the great degree of floral specialization in many species of *Moraea*, it is highly likely that there are significant differences in pollination, and, undoubtedly, there is stringent selection for certain flower characteristics and times of opening. Pollination biology in *Moraea* has been little studied and remains full of unanswered questions awaiting future study.

CONSERVATION

While most species of *Moraea* are relatively widespread within the Cape region, the genus comprises a number of very localized species. A total of 17 of the 54 species in the area treated occur within a one degree square grid. Some of these local species are known from single gatherings or from one or two populations only and can be regarded as potentially endangered species, while others have in the last 50 years been severely affected by the activities of man and his impact on the environment and are in imminent danger of extinction or even already extinct.

Possibly extinct are *Moraea incurva*, known from one gathering at the foot of the mountains between Wellington and Tulbagh, an area now under intensive cultivation, and *M. amissa*, also collected only once. A search near the type locality, north of Malmesbury, now partly a wheat field, was unsuccessful in 1974, and this species may be considered lost. The very beautiful *M. aristata*, very well represented in European herbaria and fortunately still in cultivation under the name *M. glaucopis*, is reduced in the wild to a tiny population at the Royal Observatory at Cape Town. Numbers are so low that few if any of the handful of plants at the site flower simultaneously so that reproduction rarely occurs.

Moraea insolens from Drayton siding near Caledon is also reduced to very few individuals, and the main population was recently ploughed under when the

area was planted to wheat. Individuals have been observed on the periphery of this field, but numbers are difficult to determine as this shy-flowering species blooms well only after fire (Goldblatt, 1972b). The last species imminently in danger, at least in the wild, is *M. loubseri*, known from only a single granite hill, Olifantskop, near Langebaan on Saldanha Bay. This species was only discovered recently when the hill was turned into a quarry (Goldblatt, 1976c). Efforts to introduce it to other nearby hills, and to cultivation are being made while a part of Olifantskop may be made a reserve.

A number of other species have recently been much reduced in range owing to the spread of agriculture, mainly wheat farming, on the rolling clay lowlands east and north of Cape Town, and species adapted to this habitat are becoming seriously threatened. Two species endemic to the Swartland, north of Cape Town, *Moraea neopavonia* and *M. gigandra*, both large-flowered so-called peacock moraeas fall in this category. Both were once much more common and are now reduced to a few scattered populations among the wheatlands. *Moraea debilis*, found only in the Caledon district west of Cape Town, grows in similar conditions, and the spread of agriculture here too has adversely affected this species, which almost certainly was more common in the past. Further agricultural activity will no doubt result in the extinction of these three species. Other extremely local species include *Moraea indecora*, *M. macgregorii*, *M. barnardii*, *M. tulbaghensis*, *M. nubigena*, *M. longiflora*, and *M. barkerae*. There is, however, no evidence that these were ever much more widespread than they are now, nor do they appear to be threatened at present as they grow in areas unsuitable for agriculture and away from major population centers.

Thus of a total of 54 species of *Moraea* in the southern African winter rainfall region, 2 are probably extinct, 3 more are in immediate danger, at least in the wild, although 2 of these are in cultivation, while a further 3 species can be regarded as severely reduced in range and endangered. The southwestern Cape is well known for its many very local endemics, and this small part of the world probably harbors more rare and seriously endangered species than anywhere else. Solutions to this disturbing situation are not simple as the spread of agriculture in this region is inevitable as the human population continues to expand. In the southwestern Cape an added consideration is the threat to native flora posed by weedy exotics, especially the Australian *Hakea*, *Acacia*, and *Leptospermum*, and the European *Pinus pinaster*, which have spread uncontrollably covering thousands of square kilometers and entirely choking out the native flora in many places. In this light it is difficult to see viable ways to save threatened taxa or to prevent further erosion of populations.

The introduction of species of geophytes such as Iridaceae to botanic gardens is unlikely to be a long-term solution except perhaps for the most striking species. Natural disease, predation, and neglect will almost certainly eventually eliminate species from gardens unless considerably more attention than is currently possible is devoted to the care of such plants. The establishment of many carefully managed small nature reserves throughout the southwestern Cape may prove more workable and seems in my opinion more likely to succeed.

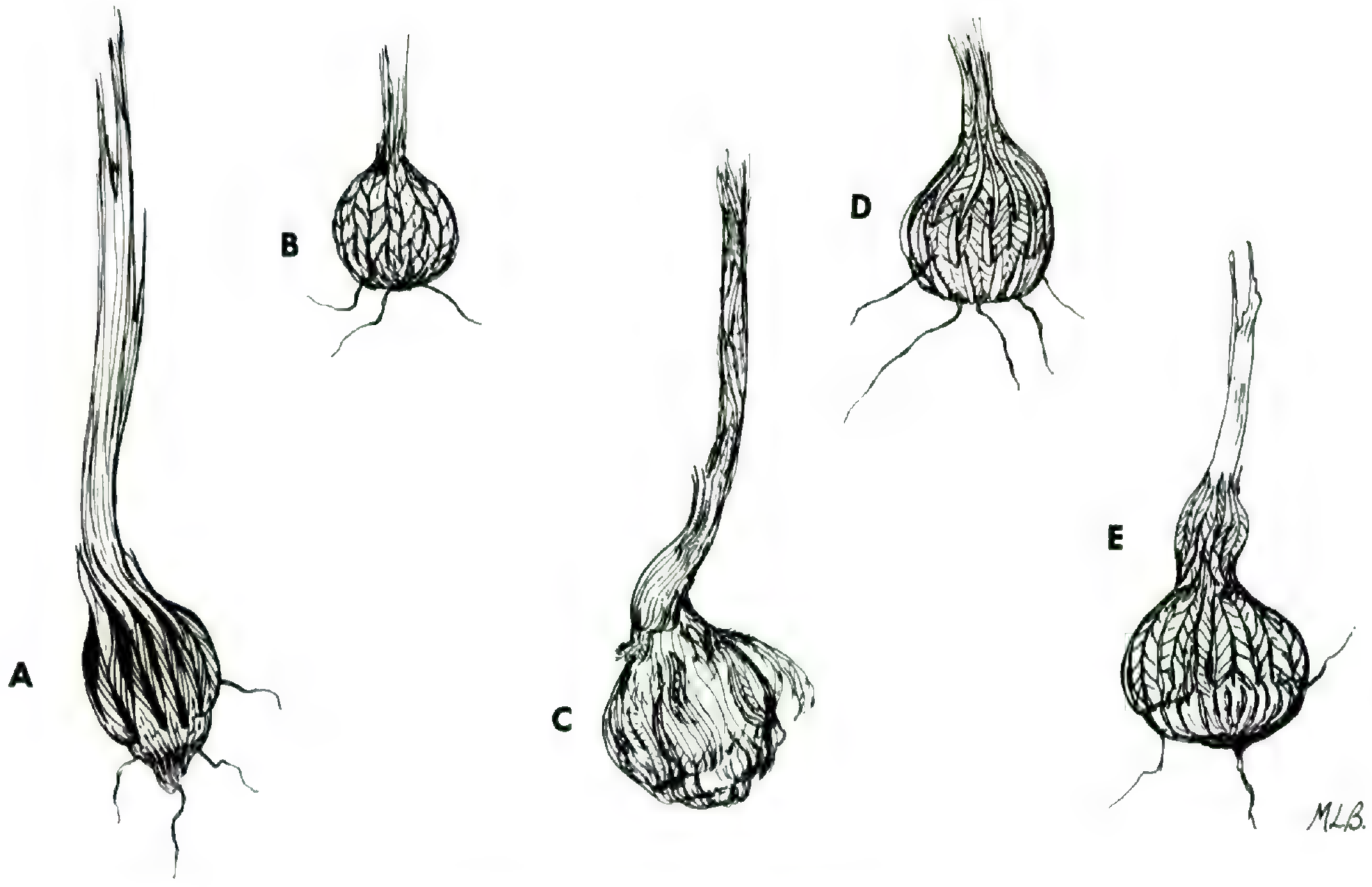

FIGURE 4. Corm types in *Moraea*.—A. *M. margaretae*.—B. *M. barkerae*.—C. *M. saxicola*.—D. *M. lurida*.—E. *M. fugax*. (× 1.5).

MORPHOLOGICAL CHARACTERS

ROOTSTOCK

In all species of *Moraea* the rootstock is a true corm (Fig. 4). This modified stem enables the plant to survive during the dormant period and is reproduced annually, developing from a lateral bud near the base of the flowering axis. It consists of a single swollen internode and, usually, a single apical bud. Unlike the corm found in subfamily Ixioideae, the roots are not produced from the corm base, but from the apical bud as this elongates when new growth begins. Apart from size differences there is little to distinguish the corm of each species.

The corm coverings or tunics (Fig. 4) are very variable, often being so distinctive as to permit specific identification. The corm tunic is of foliar origin and is the homologue of the leaf subtending the bud-derived corm. Unlike the corm, the tunics may be long lived, being fairly resistant to decay, and often accumulate round the base of the plant making the corm appear very large. Though very distinctive, most corm tunics are difficult to describe and there is no recognized terminology for the many forms that exist. Description is therefore limited to color, which ranges from black to pale; texture which may be entire and woody to membranous or heavily veined, fissured, or partly to entirely fibrous, either described as fine, medium, or coarse on an arbitrary scale.

Worthy of particular comment are the corms of several groups. The characteristic brown, ± entire, ridged, and fissured tunics in subgenus *Visciramosa* are peculiar in having a curious sticky substance covering their inner surfaces. The

tunics of subgenus *Monocephalae* are also immediately recognizable, being of a soft, almost membranous texture, dark brown, and lacerated vertically at the top and base. Coarse black fibrous tunics are uncommon but characteristic of *M. serpentina*, *M. tortilis*, *M. bolusii* and its allies, *M. polystachya*, and *M. polyanthos* (and incidentally of almost the entire genus *Homeria*).

Peculiar corms are found in *M. ramosissima* where the entire corm and numerous cormlets are surrounded by a rigid spiny network of roots. Unusual also is the corm of *M. macronyx*, distinctive in section *Acaules* in its entire tunics, composed of a spongy pithlike material.

LEAVES

Of the various foliar organs produced in *Moraea*, only the major assimilatory structures with a lamina produced above the sheathing base are referred to as leaves. The entirely sheathing basal and usually underground foliar members are called prophylls, while the sheathing cauline ones are called bract leaves or simply bracts. The paired extra-floral, inflorescence valves, here called spathes, are discussed under the inflorescence.

Prophylls.—Sheathing the underground part of the stem, the prophylls are usually membranous and transparent, or with greenish apices. Specialized prophylls occur mainly in subgenus *Grandiflora* and here they may be variously enlarged and thickened, entire or fibrous to cancellate (Goldblatt, 1973). The prophylls in most other species are undistinguished.

Leaves.—The leaf in *Moraea* and its close allies is unusual in the Iridaceae in that the typical equitant lamina is not formed, or is represented only by the very distinctive monofacial leaf apex. Instead, the sheathing base is produced upwards without a break to form a long bifacial, usually linear and channelled, blade (Arber, 1921; Lewis, 1954; Goldblatt, 1971). In a few species, e.g., *Moraea stricta*, *M. tortilis*, juvenile forms of *M. saxicola*, and subgenus *Monocephalae*, the blade is quite terete, but often still with the characteristic apical portion.

The leaves vary in number, the presence of several being regarded as primitive, and the solitary condition found in section *Deserticola*, subgenera *Monocephalae*, *Grandiflora*, and most species of *Vieusseuxia*, specialized. Leaf morphology is a useful taxonomic feature, with pubescence characteristic of certain species and usually reliable, though *M. papilionacea*, *M. tripetala*, *M. villosa*, and *M. caeca* have glabrous or villous leaves. Margins are usually straight, but typically undulate to crisped in *M. bolusii*, *M. serpentina*, *M. fergusoniae*, and most forms of *M. gawleri*. The whole leaf is markedly twisted to coiled in *M. serpentina* and helicoid in *M. tortilis*.

The leaf or lowermost leaves are usually inserted basally, near ground level, but several species have a peculiarly long basal internode so that the lowermost leaf is set well above ground level by flowering time. This gives *M. indecora* and the species of section *Subracemosae*, *M. fugax* and *M. gracilenta*, a very striking appearance. Several species of section *Polyanthes* from the summer rainfall area, e.g., *M. inclinata* and *M. natalensis*, also possess this feature.

Bract leaves.—These are produced at each aerial node and are generally en-

tirely sheathing, with an acute to attenuate apex. The bracts of subgenus *Monocephalae*, and of all species of subgenus *Visciramosa* except *M. bubalina*, are characteristically obtuse to truncate. Bracts are usually herbaceous, but apically tend to become dry and membranous with age, and the apex is often dark brown. The bracts are generally pubescent when this character occurs in the produced leaf.

STEMS

The stem or flowering scape is produced seasonally from the corm and in subgenera *Moraea* and *Visciramosa* is almost always branched. Free branching, as in *Moraea ramosissima* and *M. bituminosa*, is regarded as a primitive state, more so when the stem bears produced leaves. Branching is reduced in some species of subgenus *Moraea*, notably *M. ciliata* and its allies where the stem does not extend above ground. *Moraea falcifolia* and *M. longiflora* also have an underground stem, but both have several branches produced at ground level. Limited branching is also characteristic of many species of subgenus *Vieusseuxia*, though relatively few species regularly have a simple stem, a condition regarded as advanced. All species of subgenera *Grandiflora* and *Monocephalae* are almost always unbranched.

The stem is usually smooth and terete, but notably pubescent in *Moraea vegeta* and villous in *M. papilionacea*, *M. villosa*, *M. tulbaghensis*, *M. neopavonia*, *M. gigandra*, *M. loubseri*, and *M. debilis*.

INFLORESCENCES

The so-called binate rhipidium or corymbose cyme of the Iridaceae (excluding subfamily Ixioideae) varies little in *Moraea*. The two opposed bracts, here termed spathes, enclose several flowers, the number of which is variable. *Moraea cooperi* is unusual in this respect, having a solitary flower in each spathe. The inner spathe is always longer, sometimes considerably so, as in *M. ramosissima*. The spathes are usually herbaceous with a dry acute apex. In subgenus *Monocephalae* and often in subgenus *Visciramosa*, however, they are usually more or less obtuse. In all but the most primitive species, the spathe apex is attenuate and often dark brown. Species found in dry regions often have quite dry spathes by the time flowering takes place, and these may even become torn and lacerated, a condition often seen in *M. polystachya*, *M. serpentina*, and *M. bolusii*, amongst others.

Moraea ciliata and its close relative, *M. tricolor*, as well as *M. macronyx*, are unusual in the genus in that the true leaves and spathes are not distinct and only a single spathe can be recognized. These species are extremely reduced and highly specialized, and the loss of distinction between bracts and leaves is seen as derived.

While spathes are usually glabrous, a few characteristically villous species have a light pubescence on the spathes, particularly *M. papilionacea* and some forms of *M. ciliata*.

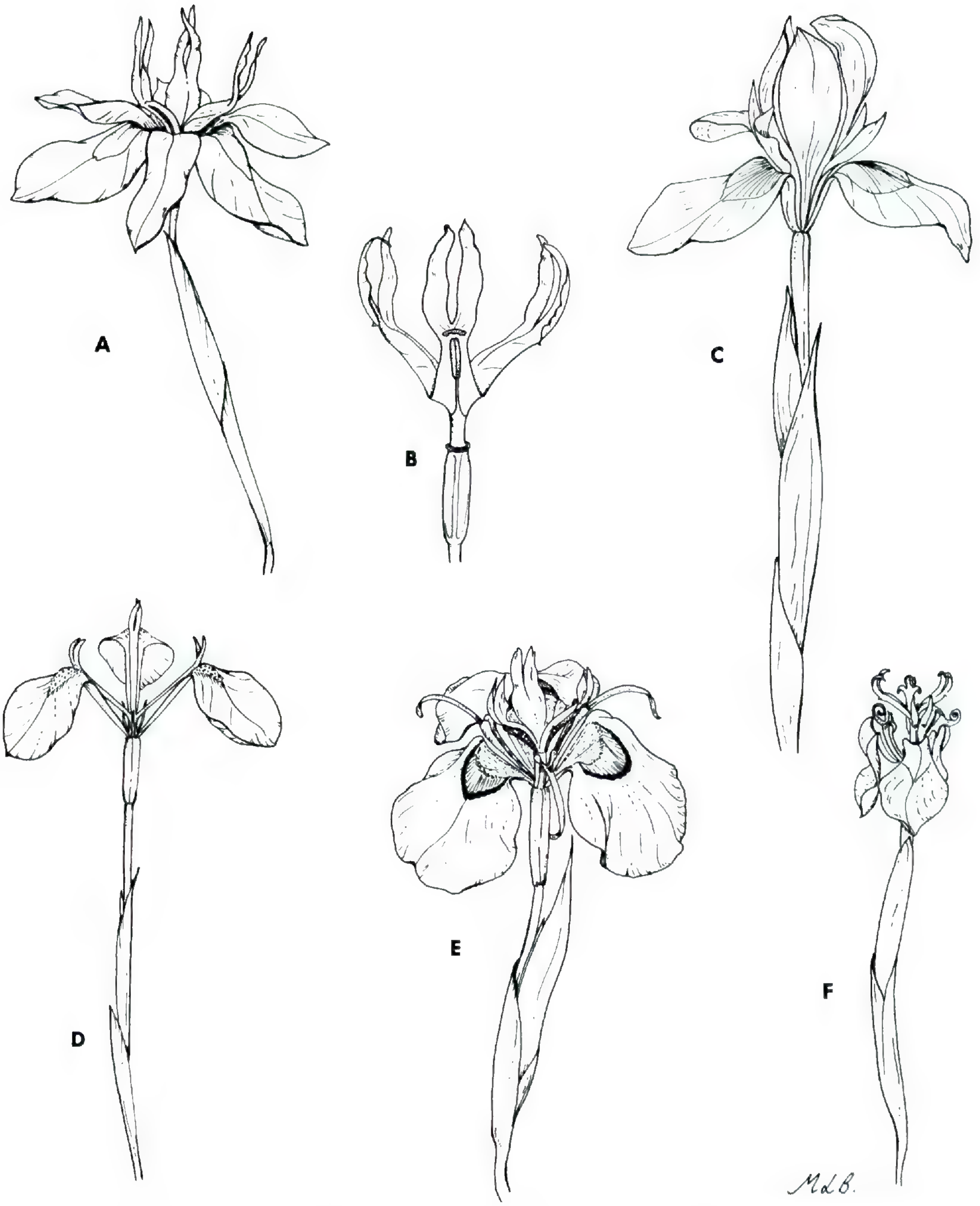

FIGURE 5. Flower morphology in *Moraea*.—A. Typically unspecialized flower of *M. polyanthos*.—B. Androecium and gynoecium.—C. Flower with erect inner tepals, *M. spathulata* (subgen. *Grandiflora*).—D. Inner tepals reduced, *M. tripetala* (subgen. *Vieusseuxia*).—E. Triscuspidate inner tepals and prominent nectar guides, *M. villosa*.—F. Triscuspidate inner tepals and reflexed outer tepals, *M. unguiculata*.

FLOWERS

The basic flower structure in *Moraea* (Fig. 5) consists of six tepals in two whorls, the outer tepals being larger and the inner somewhat to considerably smaller. The tepals are free to the base in all but two species, *M. cooperi* and

M. longiflora, where a true floral tube is developed, apparently an isolated specialization. The outer tepals are generally lanceolate in shape and consist of an erect claw and a broadened limb which is outspread to reflexed at ± 45°. A nectar guide is located at the base of the limb, frequently yellow outlined in a dark color. The claw is usually channelled and heavily pubescent and often nectiferous, with a small nectary located at its base. The inner tepals are generally narrower than the outer and not distinctly clawed, though often flexed at the midline and spread to the same degree as the outer tepals.

This floral pattern is maintained with great fidelity, particularly in the three primitive subgenera, but also in subgenus *Grandiflora* and some species in subgenus *Vieusseuxia*, and without knowledge of color, isolated flowers are of little value in determining species. Notable variations on the basic theme are in the flexure of the tepals, which in some species are very sharply reflexed from 30° to 45°, as in *M. polystachya*, *M. polyanthos*, *M. ramosissima*, *M. nubigena*, and others, while *M. inconspicua* and some forms of *M. unguiculata* (Fig. 5) have completely reflexed outer tepals. A few species have erect inner tepals, sometimes a constant feature as in *M. serpentina* or only in certain forms, as in *M. fugax*. Almost all species of subgenus *Grandiflora* have erect inner tepals.

The shape of the outer tepals is similar in the majority of species but notable exceptions occur in subgenus *Vieusseuxia*, section *Vieusseuxia* (Fig. 5E) where several species have a broad limb, often wider than long. In the group of species known as "peacock moraeas," e.g., *M. villosa* and *M. aristata*, the very broad outer tepals have a conspicuous nectar guide consisting of a yellow center ringed concentrically with broad bands of darkly contrasting color.

The inner tepals show a strong tendency towards reduction in several lines: the first indication of this is the development of a trilobed apex with a long central cusp and shorter lateral lobes. This trend is climaxed by the reduction of the inner tepal to a short cusp or by its complete absence. In subgenus *Moraea*, *M. fergusoniae* has only some populations with tricuspidate inner tepals, while in *M. cooperi* all trace of these is lacking. The majority of species in section *Vieusseuxia* have tricuspidate inner tepals, though notably not *M. thomasiae*, *M. incurva*, and forms of *M. neopavonia*, *M. barkerae*, and *M. amissa*, where the tepal may be entire. While most forms of *M. tripetala* have the tepal reduced to a short cusp, it is absent in certain populations, as well as in the allied species, *M. barnardii* (Fig. 5D).

ANDROECIUM

The three filaments are usually united for about half their length, and the free upper portion of each, as well as the anther, lie pressed against a style branch. The apex of the usually oblong anthers typically reaches to just below the single to bilobed stigma. There is some variation to the degree to which the filaments are united within species, as well as between species, but several groups are notable. In most species of section *Vieusseuxia* the filaments are relatively short but free only near the apex, for ± 1 mm. Exceptions are *M. tripetala*, *M. thomasiae*, and *M. barnardii* where the filaments are barely joined at the base.

In subgenus *Moraea*, a few populations of *M. gawleri* have free stamens and this is also the case occasionally in *M. inconspicua* (subgenus *Visciramosa*). *Moraea angusta* and *M. neglecta* also characteristically have filaments which are connate only at the base.

The anthers are similar in most species, differing only in size. Certain species, *M. gigandra*, *M. insolens*, *M. tulbaghensis*, and *M. neopavonia*, have unusually large anthers which exceed the stigma and usually also the style crests, a condition here referred to as gigandry. The reason for this adaptation is not clear but may ensure self-fertilization if cross-pollination fails to take place.

The pollen is usually yellow in *Moraea*, but certain species such as *M. tripetala*, *M. lugubris* and *M. angusta* have red pollen.

GYNOECIUM

The ovary itself is of little taxonomic value in species of the winter rainfall region and is usually ± oblong and terete. The species of subgenus *Monocephalae* and several species of subgenus *Grandiflora* have a somewhat larger ovary which is distinctly triangular to 3-winged. Above the ovary a filiform style extends the length of the filament column, and perianth tube in the case of section *Tubiflora*. The style divides at the point where the filaments diverge into three flattened branches topped by transverse, often bilobed stigmas. Each style branch bears petaloid crests which are paired, except in *M. lugubris*, where they are irregularly plumose (Fig. 14). The style crests are usually fairly large but in gigandrous species, the crests tend to be very short, sometimes less than a millimeter long and only as large as the stigmas themselves (Fig. 33).

FRUIT

The fruit is always a loculicidal capsule in *Moraea*, in shape usually narrowly clavate with a truncate apex. In the peacock species the ovary elongates considerably as it ripens, and the resulting capsule is slender and cylindrical. The capsule of *M. fugax* and *M. gracilenta* (section *Subracemosae*) is notable in being strongly beaked. A slight beak is also developed in *M. macgregorii* of section *Deserticola*. Capsules are firm walled and erect, except in *M. vegeta* and *M. indecora* where the capsule is flexed to semipendant and softer walls show the impression of the seeds.

Capsules are exserted from the spathes and are borne at their apex, except in section *Tubiflora*, where they are situated near the base of the spathes, and in section *Acaules*, where contractile pedicels draw the ovary into the spathes when the soft-walled capsule ripens.

SEEDS

There are usually many, dark brown, rounded to somewhat angular seeds in each capsule. Unusual flattened, triangular, or discoid seeds are produced in subgenus *Monocephalae* and subgenus *Grandiflora*. Seeds of the peacock species (*M. villosa* and its allies) too are unusual, tending to be large, very angular,

and with a spongy, inflated testa. Seeds of many species are unknown but their morphology may be assumed from that of their close relatives.

HISTORY OF *MORAEA*

1758–1778: THE LINNAEAN PERIOD

1758.—The history of *Moraea* begins in 1758 with Philip Miller's publication of the genus *MOREA*, in which he included three taxa described polynomially (*Figs. Pl., Tab. 238, figs. 1–2,* and *Tab. 239, fig. 1*). The first two of these are conspecific and represent the type species of the genus, *M. vegeta* L.; the third is now regarded as belonging to the genus *Dietes*. Prior to this time *Moraea* was known only through various unpublished illustrated works, the most notable of which is the *Codex Witsenii*, a collection of approximately 1,500 paintings of South African plants, amongst them several species of *Moraea*. Similar volumes possibly containing the originals of the paintings in the *Codex Witsenii* are known to be located in various libraries in Europe and South Africa (Barnard, 1947; Jessop, 1966; Macnae & Davidson, 1969). The original paintings were made during the late seventeenth century at the Cape, under the patronage of the Governor, Simon van der Stel and perhaps also of his son Willem Adrian, who was also Governor for some time. They were copied repeatedly, and a few were published in the early eighteenth century (Breyne, 1739; Burman, 1738–1739). However, none of the several paintings of species of *Moraea* was published and no species were described, even polynomially. Thus relatively few people were aware of the existence of the genus prior to 1758.

1762.—Miller's new genus was immediately adopted by Linnaeus in the second edition of *Species Plantarum* (1762), though for some reason he altered the spelling to *MORAEA* (this form now conserved against *Morea*). In this work two species, *M. vegeta* and *M. juncea*, are described with reference to Miller, though without citation of page or plate.

1766.—The publication of Daniel de la Roche's doctoral dissertation, *Plantae Novarum* . . . in 1766 is an important milestone in the history of *Moraea*. De la Roche, a student of David van Royen, the eminent eighteenth century Dutch botanist, described 21 new species of South African Iridaceae, including the new genus *Vieusseuxia* (= *Moraea* subgenus *Vieusseuxia*) with three species, all of which were in cultivation in Holland. Although aware of Linnaeus' *Moraea*, he considered his species allied but generically distinct; the three species described, *M. fugax*, *M. aristata*, and *M. bellendenii* are all somewhat different from the type species of the genus, *M. vegeta*, being slender, solitary leafed, and in the two latter species, in having tricuspidate inner tepals.

De la Roche's first species, *Vieusseuxia spiralis*, illustrated beautifully in the text, is *Moraea bellendenii* (Sweet) N.E. Brown; the earlier epithet could not be transferred to *Moraea* because the name had already been used in this genus (Linnaeus fil., 1781) for a species of *Aristea*; the second is the common Cape species *M. fugax*, long known as *M. edulis* (Goldblatt & Barnard, 1970); and the third is the very rare *M. aristata*, better known in Europe as *M. glaucopis*. Owing

to a printing error, the epithets of the second and third species of *Vieusseuxia* were transposed and this led to confusion over their interpretation. Several authors automatically corrected the obvious error, e.g., Jacquin (1776), Houttuyn (1780); others did not realize the mistake, while Lewis (1948) rejected both species on the grounds of confusion. The *Botanical Code of Nomenclature* allows for automatic correction of a printing error of this type and intended application of these de la Roche epithets was therefore revived by Goldblatt & Barnard (1970) (see also discussion under *M. aristata*, p. 773).

While I was studying the specimens associated with de la Roche's species in the Rijksherbarium, Leiden, several manuscripts containing draft descriptions of the published species came to light. The descriptions of *Vieusseuxia aristata*, progressively refined, clearly with considerable help from van Royen, reveal quite surprisingly that de la Roche began by describing the white form of *Moraea gigandra*. Van Royen obviously had a similar plant in cultivation and assumed it was de la Roche's subject, so that by the time the description was published, it was so modified as to apply to what we must now call *M. aristata*, the rare Cape Peninsula endemic.

Thus, by 1767 we know that at least four species of *Moraea* were in cultivation in Holland and at least one more in England.

1767.—No sooner had de la Roche published *Vieusseuxia* than Linnaeus (in 1767) described a third species, *M. iridioides*, clearly referring this species to Miller, *Figs. Pl., Tab. 239, fig. 1*, i.e., the rhizome-bearing *Dietes*. Later the same year, Linnaeus, in the 12th edition of the *Systema Naturae*, amplified *Moraea*, now with *M. vegeta* referred to Miller, *Figs. Pl., Tab. 238, figs. 1–2*, but *M. juncea* remained without a reference. From both Linnaeus' and Miller's treatments, it is clear that *Moraea* is a southern African genus of *iris*-like plants with both inner and outer tepals spreading and lacking a perianth tube: both cormous, bifacial-leafed and rhizomatous, equitant-leafed forms are included in this early circumscription.

The first two species which Linnaeus published, *M. vegeta* and *M. juncea*, have been the subjects of endless confusion (Barnard & Goldblatt, 1975). The complex situation is fully dealt with elsewhere, and it is sufficient here to explain that Miller, in edition 8 of *The Gardeners Dictionary*, misapplies the Linnaean epithets; thus, the name and description of *M. vegeta* is applied to *Tab. 239, fig. 1* (i.e., the rhizomatous *Dietes*, already described as *Moraea iridioides*), while *M. juncea* is applied to the second illustration on this plate, *Tritonia crocata*. There is no doubt that this was incorrect in view of Linneaus' clear referrals of *M. vegeta* to *Tab. 238* and of *M. iridioides* to *Tab. 239*; and in fact, in the abridged edition of 1771 the error is partly corrected, with *M. vegeta* applied to *Tab. 238, fig. 1*, but with the previously untypified *M. juncea* to *Tab. 238, fig. 2*. Nevertheless, Brown (1928) found reason to follow *The Gardeners Dictionary*, ed. 8, in making the combination *Dietes vegeta* (of which *M. iridioides* is a synonym). Brown also revived *M. juncea* for what is correctly *M. vegeta* [but which was at that time known by a later synonym, *M. tristis* (L.f.) Ker]. Brown's treatment was followed and as a result the nomen nudum, *M. juncea*, has come to be re-

garded as the type species of *Moraea* and is conserved as such at present in the *Botanical Code of Nomenclature*. A proposal to correct this is now in press.

Linnaeus published no further species of *Moraea*, though he did receive specimens of undescribed species from Anders Sparrman and from Carl Peter Thunberg, both of whom arrived in the Cape in 1772. Entries in Linnaeus' manuscript Mantissa no. 3 (fide Barnard, personal communication), indicate that he then intended to apply the name *M. juncea* (until that time untypified) to one of the plants which Sparrman sent him—namely what is now *M. gawleri* Spreng. After his father's death, the younger Linnaeus applied the epithet "iriopetala" to the specimen in question in his father's herbarium, and published this description in a confusing and illegitimate way under the name *M. iriopetala* var. *juncea* (for the typical variety) in the *Supplementum Plantarum*.

1778–1830: THE POST-LINNAEAN PERIOD—CLIMAX OF THE CAPZEIT IN HORTICULTURE

1778.—After Linnaeus's death in 1778, his son continued to work on the Mantissa 3, Linnaeus's unfinished manuscript which was published in 1781 as the *Supplementum Plantarum*. The younger Linnaeus added greatly to the work by borrowing from the soon-to-be-published manuscripts of Carl Peter Thunberg, and he incorporated descriptions of most of the Iridaceous plants collected by Thunberg at the Cape during a very productive 3-year period there.

The younger Linnaeus was strongly influenced by Thunberg's ideas, for he altered drastically the concept of *Moraea*, adopting Thunberg's ideas completely. The younger Linnaeus obviously did not completely understand the situation and his treatment is inconsistent. He placed under *Moraea* his father's manuscript description of *M. juncea* (i.e., of what is now *M. gawleri* Spreng.) using the epithet "*iriopetala*," including as the only varieties, *M. juncea* and *M. vegeta*. At the same time, he included under *Iris* two species taken from Thunberg's manuscripts, *Iris crispa* (= *M. gawleri* Spreng.) and *I. tristis* (= *M. vegeta* L.), the former conspecific with his *M. iriopetala* var. *juncea*.

Thunberg's concept of *Moraea* was quite different from that of Miller and Linnaeus, and he considered what we now regard as *Moraea* to be South African species of *Iris*. Thunberg's own manuscript treatment of *Iris* was published in 1782. In this work, all of the 15 South African species mentioned by the younger Linnaeus are described in detail, while 3 more are added. It is of interest to note that the form of three specific epithets differs as follows: *Iris tricuspis* Thunb. = *I. tricuspidata* L.f.; *I. spathacea* Thunb. = *I. spathulata* L.f.; *Iris setacea* Thunb. = *I. setifolia* L.f. Most, if not all, of the younger Linnaeus's species of South African *Iris* cannot be identified from his descriptions nor from a specimen in the Linnaean herbarium. The types remained in Thunberg's collection and identification is possible only by consulting Thunberg's very detailed descriptions, as well as his herbarium specimens. Strictly speaking, because of the adoption of Thunberg's specific epithets, and of the reliance on Thunberg's published work, species which the younger Linnaeus described from Thunberg's manuscript should be cited as Thunb. ex L.f. This practice has traditionally not been followed, however, and for simplicity perhaps should not be adopted.

1787.—When Thunberg published his *Dissertatio de Moraea,* he included in this genus species occurring in Asia, Africa, and the New World, and these are now considered to comprise several different genera, namely, *Homeria, Aristea, Bobartia, Ferraria, Belamcanda, Sisyrinchium,* and *Hexaglottis.* These had in common simple style branches, fugaceous flowers, subequal spreading tepals, and the absence of petaloid crested style branches of *Iris* and true *Moraea.* Thunberg however included in *Moraea* two species which are still considered to belong to this genus, and it is problematic why these two, *M. polyanthos* and *M. crispa,* were not transferred to *Iris,* as would have been consistent. Perhaps the style crests were overlooked.

Thunberg maintained his incorrect application of *Moraea* until his death, and in all his works true species of *Moraea* are treated as *Iris.* Other botanists given the lead by Jacquin [*M. fugax* (de la Roche) Jacq. 1776] soon abandoned Thunberg's view. A dichotomy in the interpretation of *Moraea* developed from Thunberg's example and lasted until 1823. The German school as successor to the Linnaean tradition (Willdenow, Sprengel, and Roemer & Schultes, etc.) used *Iris* and occasionally *Vieusseuxia* as well for species of *Moraea,* while the English school, following Ker (1803), consistently used *Moraea* in the Linnaean sense, though the genus *Vieusseuxia* was often recognized for the species with tricuspidate inner tepals (Sweet, 1830).

The post-Linnaean period is one of intense interest in Cape plants and during this time several well-known plant collectors visited the Cape, continually bringing back novelties. Among these are Masson, Lichtenstein, Burchell, Boos, and Scholl, who collected for Jacquin, as well as Drège, Ecklon, and Zeyher. Jacquin illustrated several species of *Moraea,* some for the first time, but he described no new taxa.

In England, however, important work was done by John Bellenden Ker (Ker-Gawler) who systematically revised the Iridaceae (Ker, 1805, 1827). Though at first Ker used the name *Iris,* he soon reverted to the Linnaean circumscription of *Moraea,* transferring the younger Linnaeus' and Thunberg's South African species of *Iris* to *Moraea.* Ker added four new species to the genus over a 25-year period, *M. villosa, M. lurida, M. longiflora,* and *M. unguiculata* (including *M. tenuis* which Ker believed distinct).

1808.—Ventenat published two new genera, *Homeria* and *Hexaglottis,* both based on species previously regarded as *Moraea.* This contribution was not immediately accepted, for Ker continued to regard both as synonyms of *Moraea.* Sweet (1830) does however recognize both, and subsequent treatments accepted these segregated genera.

1812.—Though R. A. Salisbury's studies on the Iridaceae are noteworthy, the eccentric way in which he published his work makes much of it nomenclaturally invalid. Salisbury was the first to suggest *Moraea iridioides* might belong to a different genus, and he proposed *Dietes,* neglecting however to provide a generic description. He is also the first to suggest that what is today recognized as *Gynandriris* might be distinct from *Iris* and from *Moraea,* to which Ker had referred the well-known Mediterranean species, *Iris sisyrinchium.* Salisbury's

Diaphane is, however, also without a proper description. A third invalid genus *Helixyra*, based on *Moraea longiflora* was subsequently used by Klatt and Baker for representatives of *Gynandriris*, although at the subgeneric level.

1827.—Ecklon's *Topographisches Verzeichniss*, in which most of the monocotyledons collected by Ecklon and Zeyher are presented, is of little taxonomic significance since it is primarily a list of collections. Several new names are used, some for new species; however, while a few can be related to known plants, almost all the species of *Vieusseuxia* (Ecklon used *Moraea* for species of *Homeria* and *Gynandriris*) are synonyms or nomina nuda.

Publication of Ker's *Iridearum Generum* (1827) closes this period. In this essentially modern treatment of the family, *Moraea* is treated with *Vieusseuxia* as synonymous and including *Hexaglottis*, *Homeria* and *Gynandriris*, but not *Dietes*. Ker included 30 species in *Moraea*, and 24 of these are still recognized in the genus. This publication established the foundation for the work on *Moraea*, and in fact for the whole Iridaceae, by J. G. Baker and F. W. Klatt in the latter half of the nineteenth century.

1830–1896: THE PERIOD OF AFRICAN EXPLORATION

The intense interest in Cape plants was on the decline with other newly explored regions providing exciting subjects for horticulture. Nevertheless, settlement in South Africa proceeded towards the interior, while exploration into tropical Africa began. It soon became evident that *Moraea* was more widespread then had till then been believed.

1844.—Specimens collected by Schimper in Ethiopia were described by Hochstetter under the genus *Hymenostigma*, but both Hochstetter's species were soon recognized as belonging to the genus *Moraea*.

1853.—Welwitch's exploration of the Portuguese territory of Angola began in 1853, and during a long period of exploration in this vast area, he discovered several species of *Moraea* in the interior highlands. It was however only much later in 1878 that Welwitch's specimens were described by J. G. Baker.

1863.—Klatt's treatments of *Moraea* are notable for the recognition of *Homeria*, *Hexaglottis*, and *Dietes* as distinct genera. In miscellaneous papers published over a 30-year period, Klatt described several new species, based on collections made by Drège and by Ecklon and Zeyher in the 1820s. Most are now regarded as synonyms of earlier names, but Klatt is to be credited with *M. falcifolia*, while *M. fimbriata* (*M. fergusoniae* L. Bol.) is a later homonym. Klatt was, however, at variance with modern treatments in recognizing *Vieusseuxia* for the tricuspidate species (section *Vieusseuxia* here).

1896.—The nineteenth century ended with the production of major floristic works and Baker's treatments of *Moraea* in the *Handbook of the Irideae* (1892), *Flora Capensis* (1896), and *Flora of Tropical Africa* (1898) still stand today as the only complete references to *Moraea*. Baker included *Vieusseuxia* as a subgenus, and treated both *Dietes* and *Gynandriris* (as *Helixyra*) at the subgeneric level. These treatments include a good representation not only from the already

well-known Cape area but from tropical African areas (now Rhodesia, Zambia, Angola and Malawi).

1896–1975: THE MODERN PERIOD

At the end of the nineteenth century the scene shifts from Europe to southern Africa where botanical activity stimulated by Harry Bolus began to bear fruit. South Africa was collected intensively, with Harry Bolus, Schlechter, and Peter MacOwan all active throughout the south. Some of their earlier discoveries were described by Baker and included in *Flora Capensis* but subsequently Louisa Bolus, Harry Bolus's niece, and G. J. Lewis, working in South Africa, added greatly to the understanding of *Moraea* in the Cape area. Louisa Bolus described nine species of *Moraea*, five recognized today, while Joyce Lewis added five species from 1933 to 1954.

At this time, plant collecting in tropical Africa, notably in Zaïre, then a Belgian colony, but also in Tanzania and Zambia, lead to the discovery of several more tropical African species. The good representation of *Moraea* in the African tropics, as well as in southern Africa, thus became increasingly evident.

1930.—The summer rainfall area of South Africa was neglected by South African botanists but this gap was filled by N. E. Brown who recognized 17 species of *Moraea* from the Transvaal, 13 of which were newly described.

1973.—As a follow-up to N. E. Brown's work on the Transvaal Iridaceae, I (Goldblatt, 1973) revised *Moraea* in the summer rainfall regions of South Africa recognizing 26 species in this area. With considerably more material at hand at this time it became evident that Brown followed too narrow a species concept, and eight of the species he recognized were reduced to synonymy.

1974–present.—With the current studies of *Moraea*, the overall understanding of the genus is now considerably clearer. The recent interest in the genus has resulted in the discovery and addition of 23 new species, as many as were correctly assigned to *Moraea* by Ker in 1827. Undoubtedly *Moraea* will yield further surprises, and several common species are still far from being perfectly understood. The study is, however, becoming urgent as the world's population expands and more land is needed for agriculture and pasture. Several species of *Moraea* in the Cape, particularly those with limited distributions, are in great danger of extinction, and even at the time of this publication, two species are in all probability extinct while another no longer occurs in the wild.

TAXONOMIC TREATMENT

Moraea Miller, Figs. Pl. 159, *tab.* 238. 1758, as *Morea* and altered to *Moraea* by Linnaeus, nom. cons. TYPE: *M. vegeta* L.

Vieusseuxia de la Roche, Diss. 31. 1766. TYPE: *V. spiralis* de la Roche = *M. bellendenii* (Sweet) N. E. Br.

Helixyra Salisb., Trans. Hort. Soc. London 1: 305. 1812, nom. nud., non sensu Baker et N. E. Br.

Freuchenia Eckl., Top. Verz. 14. 1827, nom. nud.

Phaianthes Raf., Fl. Tell. 4: 30. 1836. TYPE: *P. lurida* (Ker) Raf. = *M. lurida* Ker.

Hymenostigma Hochst., Flora 27: 24. 1844. TYPE: *H. schimperi* Hochst. = *M. schimperi* (Hochst.) Pichi-Serm.

Helixyra Salisb. ex N. E. Br., Trans. Roy. Soc. S. Africa 17: 348. 1929. TYPE: *H. flava* Salisb. = *Moraea longifolia* Ker.

Deciduous geophytic herbs. *Rootstock* a tunicate corm; tunics membranous, fibrous or reticulate. *Prophylls* several, membranous to fibrous, sheathing the underground part of stem. *Produced leaves* 1 to several, usually narrow, linear, falcate or coiled, terete or canaliculate with a minute equitant apex. *Stem* usually aerial, occasionally entirely subterranean, simple or branched, bearing reduced bractlike sheathing leaves at the upper nodes. *Inflorescence* a cymose corymb enclosed by 2 opposed spathes (occasionally 1 only); spathes herbaceous with dry acuminate apices or entirely dry, occasionally lacerated. *Flowers* several or solitary per spathe, borne serially, often fugaceous; tepals 6 (occasionally only 3) free or united in a tube in sect. *Tubiflora*; *outer tepals* unguiculate, larger than inner, marked with a conspicuous nectar guide; *inner tepals* petaloid and unguiculate, with a spreading limb, or entire and erect, or 3-lobed, cusplike, or absent. *Stamens* opposite the outer tepals and appressed to the style branches; *filaments* occasionally free or joined partly or entirely; *anthers* oblong to linear, extending to or occasionally exceeding the stigma lobe. *Style* slender, erect, branching at the apex of the filament tube; branches 3, divergent, flattened and petallike, with the stigma at the apex, above which are 2, petaloid crests (plumose in 1 species; reduced or lacking in several). *Ovary* ovoid, clavate, to linear, sometimes triangular, enclosed or emerging from the spathes. *Capsule* spherical to clavate. *Seeds* usually angled, occasionally with inflated testa, or flattened and triangular to discoid. Basic chromosome number $x = 10$; gametic numbers $n =$ 10, 9, 8, 6, 12, 20.

Distribution: montane and temperate regions of Africa south of the Sahara.

KEY TO THE SPECIES

1. Plants three to several branched; stems conspicuously sticky.
   2. Flowers large with the outer tepals more than 2.0 cm long and the spathes more than 2.5 cm long.
      3. Leaves 2 only, bracts and spathes obtuse ..... 23. *M. bituminosa*
      3.′ Leaves 2–4, bracts and spathes acute ..... 24. *M. bubalina*
   2.′ Flowers small with the outer tepals 2.3 cm long and the spathes less than 2.8 cm long.
      4. Flowers white; tepals spreading to partly reflexed, sweetly scented .. 25. *M. viscaria*
      4.′ Flowers yellow; tepals spreading or completely reflexed, not sweetly scented.
         5. Style crests minute or not developed ..... 27. *M. elsiae*
         5.′ Style crests well developed ..... 26. *M. inconspicua*
1.′ Plants simple or branched; stems not sticky.
   6. Stem entirely subterranean or barely emergent; capsules borne at ground level borne at ground level within the inflorescence spathes.
      7. Flowers borne on a perianth tube; ovary enclosed in base of the spathe ..... 22. *M. longiflora*
      7.′ Tepals ± free; ovary exserted at flowering time.
         8. Corm tunics pale; leaves and/or spathes pubescent or at least the margins ciliate.
            9. Claw of the outer tepal 1.0–1.8 cm long, ± equal to the limb.
               10. Filaments 3–4 mm long; style crests broadly triangular ..... 14. *M. tricolor*
               10.′ Filaments 5–10 mm long; style crests linear-lanceolate 12. *M. ciliata*

9.′ Claw of the outer tepal 2.5–4 cm long, 2–3 times longer than the limb ..... 13. *M. macronyx*

8.′ Corm tunics dark and coarsely fibrous; leaves not pubescent, occasionally ciliate on the margins ..... 11. *M. falcifolia*

6.′ Stem produced above ground, usually at least several cm high; capsules usually exserted from, or borne just below the apices of inflorescence spathes.

11. Produced leaves 2 or more.

12. Leaves 2 only, both produced well above the ground and inserted close together just below the first branch ..... 20. *M. fugax*

12.′ Leaves not as above, either several or if 2, at least the lower basal.

13. Stems scabrid to pubescent (occasionally very sparsely so).

14. Leaves glabrous; capsules flexed to pendant ..... 3. *M. vegeta*

14.′ Leaves usually lightly pubescent, at least with ciliate margins; capsules erect ..... 6. *M. papilionacea*

13.′ Stem glabrous.

15. Leaves coiled or undulate or with the margins undulate to crisped.

16. Filaments joined in the lower half (or free).

17. Leaf margins crisped ..... 2. *M. gawleri*

17.′ Leaf margins lightly undulate or straight (or the leaf terete).

18. Leaves channeled (rarely terete) often villous, variously coiled; inner tepals erect ..... 8. *M. serpentina*

18.′ Leaves terete, helicoid; inner tepals reflexed ..... 9. *M. tortilis*

16.′ Filaments free near the apex only ..... 5. *M. fergusoniae*

15.′ Leaves erect to falcate, the margins straight.

19. Flowers blue.

20. Style crests plumose ..... 10. *M. lugubris*

20.′ Style crests paired, entire.

21. Inner tepals reduced to a short cusp ..... 35. *M. tripetala*

21.′ Inner tepals with an expanded limb.

22. Other tepals more than 3.3 cm long; ..... 31. *M. polystachya*

22.′ Outer tepals less than 3.0 cm long; flowering August–October(–November) ..... 32. *M. polyanthos*

19.′ Flowers not blue, either yellow or cream to brick red.

23. Stems tall, branching repeatedly.

24. Inner tepals absent; tepals forming a perianth tube ..... 21. *M. cooperi*

24.′ Inner tepals well developed; tepals entirely free.

25. Leaves 3 or more.

26. Leaves produced from the base ..... 1. *M. ramosissima*

26.′ Lower part of the stem leafless, lower leaves inserted well above ground ..... 4. *M. indecora*

25.′ Leaves 1 or 2 ..... 2. *M. gawleri*

23.′ Stems short, branching from near the base only or from the lowest aerial node.

27. Leaf ± erect, the margins straight ..... 7. *M. margaretae*

27.′ Leaf somewhat twisted, the margins undulate ..... 5. *M. fergusoniae*

11.′ Produced leaves solitary.

28. Inner tepals entire, the limb expanded, ensiform to lanceolate or ovate (not trilobed-tricuspidate).
    29. Leaf inserted well above ground level just below the first branch; ovary and capsule beaked.
        30. Outer tepals 1.8–2.8 cm long; spathes 2.5–4 cm long; plants more than 30 cm high ..... 19. *M. gracilenta*
        30.′ Outer tepals 2.8–4.0 cm long; spathes 4–8 cm long; if tepals shorter, then plants less than 20 cm high ..... 20. *M. fugax*
    29.′ Leaf ± basal or inserted shortly above ground level; capsule rarely beaked.
        31. Leaves terete.
            32. Inflorescence spathes and bracts acute-acuminate; ovary not angular-winged.
                33. Leaf coiled below the apex only ..... 15. *M. saxicola*
                33.′ Leaf uniformly coiled throughout its entire length ..... 9. *M. tortilis*
            32′. Inflorescence spathes and bracts often obtuse to truncate; ovary angular to winged.
                34. Filaments joined at the base only (less than 2 mm).
                    35. Style branches exceeding the crests; nectar guide lined with dots ..... 30. *M. neglecta*
                    35.′ Style branches not exceeding the crests; nectar guide clear, circled with darker color ..... 28. *M. angusta*
                34.′ Filaments joined at least 3 mm and up to half their length ..... 29. *M. anomala*
        31.′ Leaves channeled.
            36. Stamens exceeding the style crests.
                37. Stem and usually leaves pubescent ..... 46. *M. neopavonia*
                37.′ Stem and leaves glabrous ..... 43. *M. insolens*
            36.′ Stamens not exceeding the style crests.
                38. Outer tepals exceeding 3.5 cm, and inflorescence spathes more than 8 cm long ..... 54. *M. spathulata*
                38.′ Outer tepals less than 3.5 cm long, or if longer spathes no more than 7 cm long.
                    39. Inner tepals erect and not as long as the style branches ..... 34. *M. algoensis*
                    39.′ Inner tepals much longer than the style branches, not necessarily erect.
                        40. Filaments united almost to the apex, free for ± 1 mm.
                            41. Filaments 3–4 mm long.
                                42. Spathes ± 4 cm long ..... 50. *M. amissa*
                                42.′ Spathes 1.2–1.4 cm long ..... 33. *M. nubigena*
                            41.′ Filaments more than 5 mm long.
                                43. Limb of outer tepals longer than the claw ..... 38. *M. incurva*
                                43.′ Limb of outer tepals shorter than the claw ..... 42. *M. lurida*
                        40.′ Filaments not united to the apex, at least the upper third free.
                            44. Leaf with thickened hyaline margins.
                                45. Anthers ca. 4 mm long; outer tepals no more than 8 mm wide ..... 16. *M. macgregorii*

45.′ Anthers more than 5 mm long; outer tepals more than 1 cm wide.
46. Leaf seldom exceeding 20 cm, with markedly undulate margins; flowers usually yellow ---------- 18. *M. bolusii*
46.′ Leaf more than 25 cm long, occasionally with slightly undulate margins; flowers white to pale blue ---- 15. *M. saxicola*
44.′ Leaf margins not thickened.
47. Filaments free almost to the base ---------- 40. *M. thomasiae*
47.′ Filaments united for half to two-thirds of their length.
48. Filaments 1.3–1.5 cm long; mountains of the western Cape ---------- 39. *M. barkerae*
48.′ Filaments up to 1 cm long; southern South West Africa ---------- 17. *M. namibensis*

28.′ Inner tepals either trilobed to tricuspidate, or filiform to minute or absent.
49. Filaments united for at least half their length, usually free near the apex only.
50. Stem and/or leaf pubescent.
51. Anthers much exceeding the style crests.
52. Style crests obsolete, not exceeding the stigma ---------- 47. *M. gigandra*
52.′ Style crests ca. 2 mm long, extending above the stigma ---------- 46. *M. neopavonia*
51.′ Anthers shorter than the style branches or barely exceeding them, but not exceeding the style crests.
53. Inner tepals filiform; stem glabrous ---- 36. *M. debilis*
53.′ Inner tepals flattened and grooved below; stem pubescent.
54. Flowers orange; style crests ca. 2 mm long ---- 52. *M. tulbaghensis*
54.′ Flowers blue, purple, pink, or cream; style crests usually exceeding 3 mm.
55. Outer tepals with the claw and part of the limb heavily bearded; nectar guide obscure and without a yellow eye ---------- 53. *M. loubseri*
55.′ Outer tepals not black bearded.
56. Outer tepals at least 3 cm long and with a conspicuous nectar guide of yellow surrounded by a broad dark band ---------- 51. *M. villosa*
56.′ Outer tepals not exceeding 2.8 cm and with a very small nectar guide, either yellow or dark ----- 48. *M. caeca*
50.′ Stem and leaf glabrous.
57. Filaments exceeding 1 cm, free in the upper third ---- 39. *M. barkerae*

57.′ Filaments less than 1 cm long, usually free near the apex only.
58. Flowers blue-violet.
59. Inner tepals exceeding the stigmas ..... 50. *M. amissa*
59.′ Inner tepals not reaching the stigmas ..... 34. *M. algoensis*
58.′ Flowers not blue-violet.
60. Inner tepals with the central cusp linear and outspread, much exceeding the lateral cusps or lobes.
61. Flowers white with a large dark nectar guide with a large yellow or blue center ..... 49. *M. aristata*
61.′ Flowers purple with a very small black or yellow nectar guide ..... 48. *M. caeca*
60.′ Inner tepals with the central cusp tapering, or if linear, then coiled inwards and not exceeding the lateral lobes more than twice.
62. Outer tepals cupped to ± outspread; 2.5–3.5 cm long.
63. Claw of outer tepals glabrous to papillate ..... 42. *M. lurida*
63.′ Claw of outer tepals pubescent.
64. Filaments 3–5 mm long; flower yellow .. 45. *M. bellendenii*
64.′ Filaments 5–6 mm long; flower white-cream ..... 44. *M. tricuspidata*
62.′ Outer tepals sharply reflexed from 45° to 90°; seldom exceeding 2.2 cm in length ..... 41. *M. unguiculata*
49.′ Filaments united near the base only or for less than a third of their length.
65. Flowers white, marked with blue; tepal margins lightly crisped ..... 37. *M. barnardii*
65.′ Flowers blue to purple not speckled; tepal margins not crisped ..... 35. *M. tripetala*

I. Subgenus MORAEA

Subgenus **Moraea**. TYPE: *Moraea vegeta* L.

Plants small to large, several to many branched, the stem rarely simple. *Corm* tunics various, never bituminous. *Leaves* solitary to several. *Stem* produced above ground or entirely subterranean; nodes smooth. *Flowers* generally unspecialized; inner tepals entire, spreading, occasionally reduced and tricuspidate or lacking. *Capsules* exserted or enclosed, spherical, clavate or cylindrical, beaked in a few species; *seeds* small, rounded to angular. Basic chromosome numbers, $x = 10, 9, 8, 6$.

Distribution: Entire winter rainfall area from southern South West Africa in the north to Grahamstown in the east, with a few species extending into the summer rainfall areas of the karoo and East Griqualand.

Subgenus *Moraea* comprises a rather heterogeneous assemblage of species. While there is a variety of vegetative habits, flowers of most species are similar

and quite unspecialized with comparatively large, entire tepals. Uniform floral morphology as well as a distinctive series of karyotypes serve to unite this group. All the species in the subgenus with the basic chromosome number $x = 10$ have 3–5 long acrocentric chromosome pairs and a corresponding number of much smaller ones.

The many-leafed and branched habit is regarded as ancestral in *Moraea*, and section *Moraea* probably stands in such a position, not only in subgenus *Moraea* but to the specialized subgenera *Grandiflora* and *Vieusseuxia* that have reduced branching, a single leaf, and the derived basic chromosome number, $x = 6$. Morphological features of subgenera *Monocephalae* and *Visciramosa*, which like subgenus *Moraea* have $x = 10$, make it unlikely that they are directly related to section *Moraea*, and all three are probably derived from an extinct common ancestor.

The few species with chromosome numbers lower than $n = 10$ have derivative karyotypes as a result of chromosomal rearrangements accompanying the aneuploid reduction.

Section 1. **Moraea**. TYPE: *Moraea vegeta* L.

Moraea subgenus *Eumoraea* section *Corymbosae* Baker, Fl. Cap. 6: 10. 1896.

Plants small to large, several to many branched. *Corm* tunics of light or dark, fine to coarse fibers. *Leaves* 2 to several, basal and/or cauline. *Stems* rarely simple, usually several branched. *Flowers* usually with all tepals reflexed or outspread; inner tepals usually entire, occasionally tricuspidate. *Capsules* spherical to clavate, exserted; *seeds* small, angular. Basic chromosome numbers $x = 10, 9, 8$.

Distribution: Entire winter rainfall area from Grahamstown in the east to Namaqualand.

Section *Moraea* comprises a varied range of species, all of which have more than a single leaf and are usually several branched. The base number is $x = 10$ excepting *M. papilionacea* with $n = 9$ and *M. indecora* with $n = 8$. *Moraea margaretae* with $n = 20$ is the only polyploid species in the section.

1. **Moraea ramosissima** (L.f.) Druce, Bot. Soc. Exch. Club. Brit. Isles. 4: 636. 1914.

Iris ramosissima L.f. Suppl. Pl. 99. 1781. TYPE: South Africa, Cape, sandy places in the Swartland, *Thunberg s.n.* (Herb. Thunberg 1169, UPS, lectotype).
I. ramosa Thunb., Diss. Irid. no. 24. 1782. TYPE: As for *I. ramosissima* L.f.
Moraea ramosa (Thunb.) Ker, Bot. Mag. *tab. 771*. 1804; Baker, Fl. Cap. 6: 1896.
M. bulbifera Jacq., Hort. Schoenb. 2: 38, *tab. 197*. 1797. TYPE: Illustration in Hort. Schoenb. *tab. 197* (lectotype).
Freuchenia bulbifera Eckl., Top. Verz. 14. 1827, nom. nud.
Vieusseuxia freuchenia (Eckl.) Steud., Nom. Bot. 2: 765. 1841, nom. inval.

Plants large, 50–120 cm, much branched. *Corm* 2–3 cm in diameter, producing many cormlets round the base; rootstock enclosed in a network of spinous roots. *Leaves* many, distichous, canaliculate, to 30 cm long and 1.5 cm wide, falcate. *Stem* terete or grooved above the nodes, branching repeatedly from the

base to the apex. *Spathes* herbaceous with dry, acute to attenuate apices; inner spathe 2–2.5 cm long, the outer much shorter, less than 1 cm long. *Flowers* few per spathe, bright yellow; tepals all reflexed to 45°, the outer somewhat larger than the inner, ca. 3 cm long and to 1.5 cm wide. *Filaments* 12–15 mm long, entirely free or joined near the base only; *anthers* ca. 1 cm long. *Style branches* 2–2.5 cm long, the crests linear-lanceolate. *Capsule* ± spherical, truncate at the apex, ca. 6 mm in diameter; *seeds* angled. Chromosome number $2n = 20$.

Flowering time: October to December, typically late flowering.

Distribution: Widespread in moist places in sandy soils, mountains and flats from the Cedarberg in the north to Grahamstown in the east.—FIG. 7.

Moraea ramosissima, a species known for some time by the synonym *M. ramosa*, is one of the tallest in the genus. It is regarded as the most primitive species of *Moraea* because of its numerous leaves, abundant branching, and the unspecialized nature of the flower. Its very distinctive habit and size ensure that it is never confused with other species. Its closest relative is probably *M. gawleri*, a much smaller plant, which is similar in having a branched axis and small inflorescence spathes.

Moraea ramosissima has the unique characteristic in the genus of spinous roots, a feature described in detail by Lewis (1954). The modified roots form a basketlike network around the corm and probably have a protective function. They do not however prevent massive depradations by baboons, who uproot large numbers of plants in search of the corms. The survival of such populations is assured by the production of cormlets which *M. ramosissima* sheds in large numbers from the base of the main corm and also from the lower aerial nodes.

Moraea ramosissima is comparatively widespread within the winter rainfall area and occurs primarily in mountain areas, always in wet situations, either along streams, seepage zones, or below cliffs. It ranges from the Giftberg and Cedarberg in the north to Grahamstown in the east and is particularly abundant on the Cape Peninsula.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): Giftberg Mountain (D), *Bayliss 6098* (MO).

32.18 (Clanwilliam): Near Clanwilliam (BB), *Galpin 10514* (BOL, BR, PRE); *Leipoldt s.n.* (SAM-20579).

32.19 (Wuppertal): Elandskloof (CA), *Lewis 842* (SAM). Warm Baths, Olifants River valley, *Edwards s.n.* (BOL-14416).

33.18 (Cape Town): Claremont, Cape Town (CD), *Wolley Dod 504* (BOL, K). Kirstenbosch, *Bolus 3261* (BOL). Skeleton Gorge, *Leighton 737* (BOL). Blinkwater, *Cassidy 86* (NBG). Head of Jonkershoek valley (DD), *Esterhuysen 9700* (PRE).

33.19 (Worcester): Winterhoek, Tulbagh (AA), *Pappe s.n.* (SAM-25174). Grootwinterhoek, *Marloth 1728* (PRE). Bains Kloof (CA), *Gillet 4518* (BOL). Baviaans Kloof, *Lewis 982* (SAM). Zachariashoek, Kasteels Kloof (CC), *Smith 63* (PRE). Louwshoek mountains (CD), *Stokoe s.n.* (SAM-58746).

33.20 (Montagu): Below 10 o'clock Peak (CD), *Wurts 452* (NBG). Grootvadersbosch (DD), *Jackson s.n.* (NBG-58808).

33.22 (Oudtshoorn): George (CD), *Sister Stephany s.n.* (BOL). Montagu Pass, *Penther 757* (M, S). Karatara, Zuur Rug (DD), *Keet 1151* (GRA).

33.23 (Willowmore): Ratelsbosch, Tsitsikama Forest (DC), *Fourcade 370* (BOL, GRA).

33.24 (Steytlerville): Groot River (DA), *Barker 6056* (NBG).

33.25 (Port Elizabeth): Witteklip (CC), *MacOwan 399* (BOL, K).

33.62 (Grahamstown): Grahamstown (BC), *MacOwan s.n.* (SAM-20580). Howisons Poort, *Britten 2826* (GRA).

34.18 (Simonstown): Smiths Farm, Cape Peninsula (AD), *Barker 7171* (NBG). Brightwater, Cape Point Nature Reserve, *Lewis 2278* (SAM). Sir Lowry's Pass (BB), *Rogers 26950* (PRE) Arieskraal (BD), *Barker 3357* (NBG). Porter Reserve, Bettys Bay, *Ebersohn 138* (NBG).

34.19 (Caledon): Near Bot Rivier (AA), *Schlechter s.n.* (PRE). Onrus River (AC), *Gillet 4399* (BOL, MO). Riviersonderend (BB), *Zeyher s.n.* (SAM-48586); *Ecklon & Zeyher 1645* (S).

34.23 (Knysna): Storms River mouth (BB), *Acocks 21179* (PRE).

2. **Moraea gawleri** Spreng., Syst. Veg. 5 (Index): 462. 1828, nom. nov. pro *M. crispa* (L.f.) Ker.—Fig. 6A–C.

M. crispa (L.f.) Ker, Bot. Mag. *tab. 754.* 1804; Baker, Fl. Cap. 6: 15. 1896, incl. var., non Thunb. 1787, hom. illeg.

M. crispa var. *rectifolia* Baker, Fl. Cap. 6: 16. 1896. TYPE: South Africa, Cape, Table Mountain, *H. Bolus 4718* (BOL).

Iris crispa L.f., Suppl. Pl. 98. 1781. TYPE: South Africa, Cape, hills near Cape Town, *Thunberg s.n.* (Herb. Thunberg 1120, UPS, lectotype; S, isolectotype)

Moraea undulata Ker,[5] Irid. Gen. 43. 1827, nom. nov. pro *M. crispa* (L.f.) Ker, hom. illeg., non *M. undulata* (L.) Thunb., 1787.

Vieusseuxia brehmii Eckl., Top. Verz. 12. 1827, nom. nud.

V. angustifolia Eckl., Top. Verz. 12. 1827, nom. nud.

Moraea decussata Klatt, Abh. Naturf. Ges. Halle 15: 367. 1882. TYPE: South Africa, *Krauss 1447* (V, holotype, destroyed; authentic material at S).

M. sulphurea Baker, Bot. Mag. *tab. 7658.* 1889. TYPE: Illustration in Bot. Mag. *tab. 7658.*

Plants 15–45 cm high, usually several branched. *Corm* 5–15 mm in diameter; tunics usually light brown, the fibers coarse and vertically ridged. *Leaves* 2 (rarely 1 only), the lower basal, the upper produced from the lowest aerial node; linear and ± erect or spreading and somewhat coiled, the margins plane, undulate or crisped, glabrous, 1–6 mm wide. *Stem* rarely simple, usually 3–5-branched. *Spathes* herbaceous or dry towards the apex, acute, seldom attenuate; inner spathe 1–2.5 cm long, the outer ca. half the length of the inner. *Flowers* few per spathe, yellow, cream or pale brick; outer tepals 1.2–2.8 cm long, the claw somewhat less than half, the limb 0.5–1.4 cm wide; inner tepals 1–2 cm long, also reflexed. *Filaments* ca. 6 mm long, united for ca. half their length; *anthers* 2–3 mm long, red or yellow. *Style* branched at the apex of the filament tube, the branches to 8 cm long, the crests lanceolate. *Capsule* ± spherical, ca. 5 mm in diameter; *seeds* angular. Chromosome number $2n = 20$, $2n = 24$, 26 ($x = 10$).

Flowering time: July to September, to October in the south.

Distribution: Clay flats and slopes, usually in Renosterbosveld, occasionally in sandy situations, widespread from Namaqualand in the north to Humansdorp in the east.—Fig. 7.

The rather small, slender *Moraea gawleri* is most easily recognized by its small inflorescence spathes, the outer of which is seldom more than 1 cm long. Though 2 crisped leaves are the rule, both solitary-leafed, and straight-margined forms occur, the latter in moister habitats. The straight-margined form, described

[5] Baker used this name for the true *M. crispa* Thunb. and not in Ker's sense (Fl. Cap. 6: 19. 1896.).

FIGURE 6. *Moraea* species.—A–C. *M. gawleri*.—A. Habit (×0.3).—B. Flower (life size).—C. Style branch and stamen (×2).—D–F. *M. ramosissima*.—D. Habit (×0.25).—E. Flower (life size).—F. Style branch and stamen (×2).

as *M. crispa* var. *rectifolia* by J. G. Baker, is not recognized in this treatment as there are populations in which all possible leaf types from straight edged to very crisped occur side by side, indicating that the variety has no taxonomic validity. *Moraea gawleri* is most closely allied to *M. ramosissima*, though it is a much

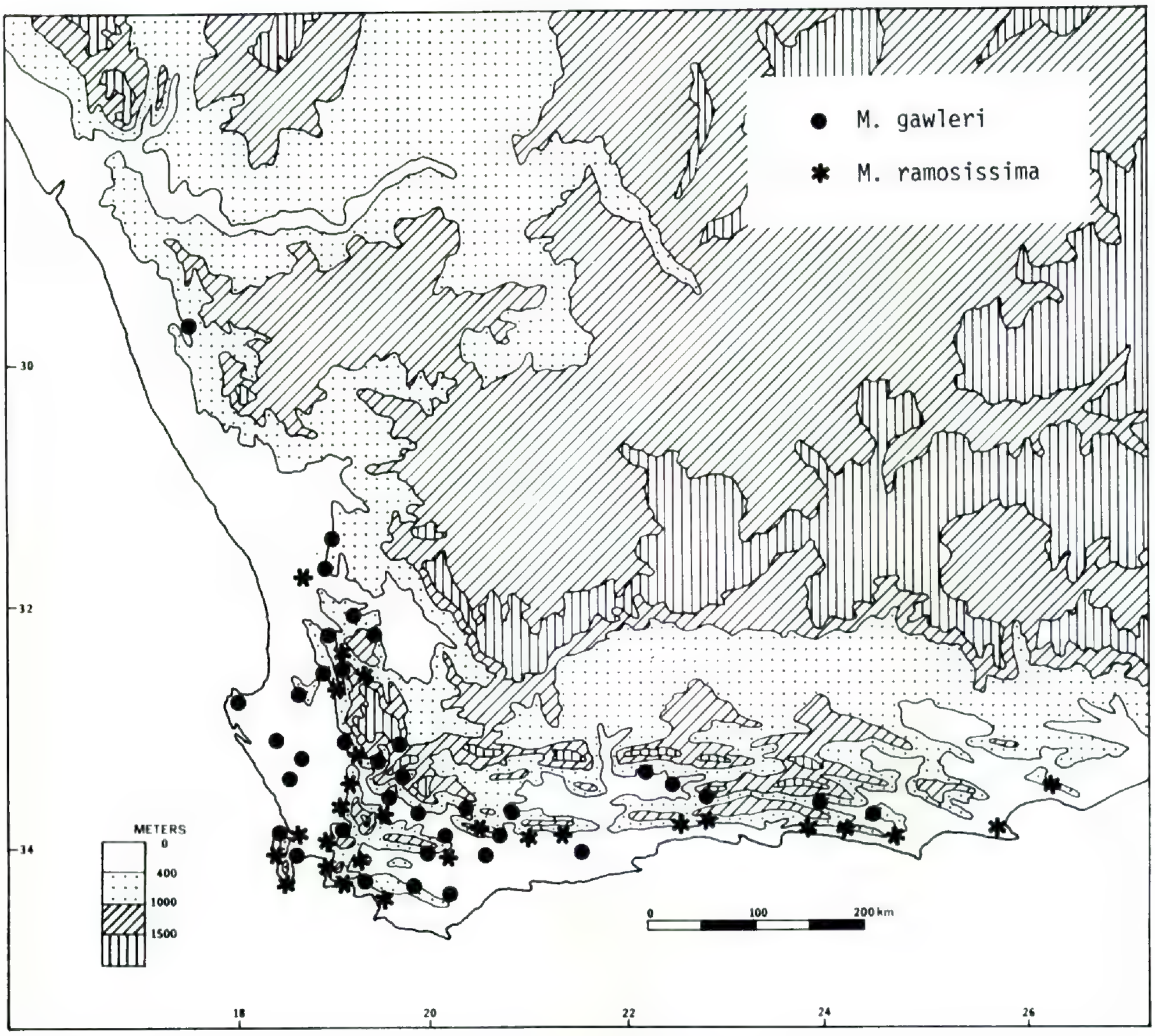

FIGURE 7. Distribution of *Moraea gawleri* and *M. ramosissima*.

smaller plant. Flowers are usually a bright yellow to buff color, but a brick red form is found along the west coast in dry situations as far north as Nieuwoudtville. Occasionally populations with red tepals and yellow style crests are encountered, notably in the south where the red and yellow colored forms both occur.

Moraea gawleri has perhaps the widest range of the Cape species of *Moraea* and occurs over almost the entire winter rainfall zone. It is represented by a relict population on Spektakelberg, west of Springbok in Namaqualand, and occurs almost continuously from Nieuwoudtville to the Cape Peninsula and eastwards to the Longkloof in the Humansdorp district. Except on the Cape Peninsula where it does grow in sandy situations, it is confined to clay soils and is often found in rather dry places.

Originally described as *Iris crispa* L.f., based on a Thunberg collection, this plant has had an unfortunate taxonomic history. *Moraea crispa* Thunb., quite a different plant, blocks the legitimate transfer of *Iris crispa* to *Moraea*. When Ker (1827) realized his error in transferring the species to *Moraea*, he proposed the new name *M. undulata*. This also proved to be a homonym, for *M. undulata*

(L.) Thunb. (the familiar *Ferraria undulata*). Sprengel provided the name *M. gawleri*, the second new name given to this plant, and the one which must now be used. In spite of its being a homonym, *M. crispa* (L.f.) Ker was applied to this species in *Flora Capensis* by J.G. Baker who also ignored Klatt's *M. decussata*, a new species, which the latter author evidently intended to replace the illegitimate combination *M. crispa* (L.f.) Ker.

Baker's *M. sulphurea* is somewhat hesitantly included here as a synonym of *M. gawleri*. The type illustration agrees generally with this species, but it is unusual in having no branches, and the leaves are without the usual crisping. These discrepancies may, however, be due to the affects of cultivation rather than indicative of any fundamental differences between *M. sulphurea* and more usual forms of *M. gawleri*.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Spektakelberg (DA), *Goldblatt 627* (BOL); *Thompson 1020* (PRE, STE).

31.18 (Van Rhynsdorp): Giftberg plateau (DC), *Barker 9593* (NBG); *Goldblatt 359* (BOL). Olifants River barrage (DD), *Barker 1332* (NBG).

31.19 (Calvinia): Near Nieuwoudtville (AC), *L. Bolus s.n.* (BOL-19838). Top of Van Rhyns Pass, *Goldblatt 223* (BOL). 20 km SW of Nieuwoudtville, *Acocks 19473* (BOL, M, NBG).

32.17 (Vredenburg): Steenberg's Cove (DB), *Taylor 1531* (SAM).

32.18 (Clanwilliam): Near Clanwilliam Dam (BB), *Stokoe s.n.* (SAM-60191). Nardouw Pass, *Stokoe s.n.* (SAM-55677). Alpha, at Algeria turnoff (BD), *Goldblatt 288* (BOL). Kapteins Kloof, Piketberg (DC), *van Niekerk 622* (BOL). Near Piketberg (DD), *Barnes s.n.* (BOL); *Lewis s.n.* (BOL).

32.19 (Wuppertal). Welbedacht, Cedarberg (AA), *Barker 263* (NBG). Bidouw valley pass, *Thompson 340* (PRE, STE). Warm Baths, Olifants River valley (CA), *Edwards s.n.* (BOL-14435). *Leipoldt s.n.* (BOL, K), *Pearson 7338* (K).

33.18 (Cape Town): Zout River, Hopefield (AB), *Garside 1602* (K). Darling (AD), *H. Bolus s.n.* (BOL, BR). Mamre hills, *van Niekerk 262* (NBG); *Barker 3843* (BOL, NBG). Moorreesburg (BA), *H. Bolus 9990, 9988* (BOL, BR, PRE). Kenilworth, Cape Peninsula (CD), *H. Bolus s.n.* (BOL). Signal Hill, Cape Peninsula, *Wolley Dod 1599* (BOL, K); *H. Bolus 4980* (BOL); *Marloth 1557* (PRE); *Page s.n.* (BOL-16754). Table Mountain above Klaasenbosch, *H. Bolus 4718* (BOL). Agter Paarl (DB), *Barker 431* (NBG). Swartboskloof, Jonkershoek (DD), *Lewis 1651* (BOL, SAM). Onderpapegaaisberg, *Taylor 5031* (PRE, STE).

33.19 (Worcester): De Hoek, Saron (AA), *Barker 5852* (NBG). Tulbagh Road, station (AC), *Goldblatt 218* (BOL). Karoopoort (BA), *L. Bolus s.n.* (BOL-19916). Hottentots Kloof, *Barker 3020* (NBG). Lakenvlei (BC), *Barker 1331* (NBG). De Doorns, Hex River valley, *H. Bolus 13194* (BOL); *Marloth 2010* (PRE). Near Worcester (CB), *Leipoldt s.n.* (BOL). Karoo Garden, *Stayner s.n.* (NBG-90759); *Olivier 106* (PRE, STE). Rabiesberg (DA), *Lewis s.n.* (BOL). 3 km E of Robertson (DD), *Acocks 16106* (PRE).

33.20 (Montagu): Keur Kloof, Montagu (BC), *Compton 5697* (NBG). Bonnievale (CC), *Dymond s.n.* (BOL); *Marloth 11825* (PRE). Below Crown Mountain, Swellendam (CD), *Barker 277* (NBG); E of Barrydale (DC), *Hall 1432* (NBG).

33.22 (Oudtshoorn): Ca. 30 km E of Camphor Station, Longkloof (DC), *Mauve 4572* (PRE, STE). Near Keurbooms River, Longkloof (DD), *Fourcade 4689* (BOL, SAM).

33.24 (Steytlerville): Bo Plaas, *Bayliss 5969* (NBG, MO, PRE).

34.18 (Simonstown): Above Llandudno, Cape Peninsula (AB), *Salter 6240* (BOL, K); *Hafstrom & Acocks 317* (PRE). Cape Point Reserve (AD), *Compton 18300* (BOL, NBG).

34.19 (Caledon): Near Hermanus (AC), *H. Bolus s.n.* (BOL). 21 km E of Caledon (BA), *Story 3072* (PRE). Riviersonderend (Appelskraal) *Zeyher 4088* (PRE). Napier (BD), *Bond 476* (NBG).

34.20 (Bredasdorp): Bontebok Park, Swellendam (AB), *Liebenberg 6457* (PRE, STE). Tradouw Pass (BA), *Marloth 8628* (PRE). Bredasdorp (CA), *Loubser 888* (NBG).

34.21 (Riversdale): Near Riversdale (AB), *Muir 2687* (BOL).

3. **Moraea vegeta** L.,[6] Sp. pl., ed. 2. 59. 1762; Syst. Nat., ed. 12. 78. 1767. TYPE: Illustration in Miller, Figs. Pl. 2, *tab.* 238. 1758.—FIG. 8.

Iris tristis L.f. Suppl. P. 97. 1781. TYPE: South Africa, Cape, below Devils Peak, near Cape Town, *Thunberg s.n.* (Herb. Thunberg 1190, UPS, lectotype).
Moraea tristis (L.f.) Ker, Ann. Bot. (König & Sims) 1: 241. 1805; Baker, Fl. Cap. 6: 18. 1896.
Ferraria tristis (L.f.) Salisb., Prodr. Stirp. 42. 1796.
Moraea iriopetala L.f., Suppl. Pl. 100. 1781, nom. illeg., superfl. pro *M. vegeta* L.
M. sordescens Jacq., Ic. Pl. Rar. *tab.* 225. 1795; Coll. 5: 29. 1797. TYPE: Illustration in Jacq., Ic. Pl. Rar.
Vieusseuxia graminifolia Eckl., Top. Verz. 11. 1827. TYPE: South Africa, Cape, "Groene Berg," *Zeyher 1068* (S, lectotype).
V. rivularis Eckl., Top. Verz. 11. 1827, nom. nud.
"*Moraea juncea* L." sensu N. E. Brown, J. Linn. Soc. Bot. 48: 42. 1928.

Plants (10–)15–30 cm high, usually several branched. *Corms* 1–2 cm in diameter; tunics of fine, pale fibers. *Leaves* several, produced from the base and the aerial nodes, the lower linear, exceeding the inflorescence, glabrous, glaucous, often dry and torn at the apex. *Stem* several branched, markedly puberulous. *Spathes* herbaceous, occasionally with brown apices; inner spathes 2–4 cm long, the outer 1.5–3 cm. *Flowers* few per spathe, dull yellow to brown, flushed with blue or purple; outer tepals 2–2.5 cm long, lanceolate, the limb to 1.8 cm long; inner tepals smaller, also reflexed. *Filaments* 5–6 mm long, joined in the lower third; *anthers* 3–4 mm, acute, blue. *Style branches* 7–8 mm long, the lanceolate crests 7–10 mm long. *Capsule* ± spherical, soft walled and showing impression of seeds, pendulous when mature, ca. 8 mm in diameter; *seeds* round to angular. Chromosome number $2n = 20$.

Flowering time: September and October.

Distribution: Common on the Cape Peninsula and north to the Darling area on heavy, usually clay soils; also recorded from the Swellendam and Tulbagh districts.—FIG. 8.

Moraea vegeta with its several characteristic glaucous leaves, puberulous stem, and somewhat pendulous capsules is not easily confused with related species with similar flowers such as *M. papilionacea* and *M. gawleri*. Its closest allies are probably *M. papilionacea* whose range covers that of *M. vegeta*, and also the newly discovered *M. indecora*, known only from the area near Springbok in Namaqualand. *Moraea indecora* is a large species which has a similar subpendulous capsule; its smooth elongated stem and large red stamens are, however, quite different from those of *M. vegeta*.

Moraea vegeta is one of the few species of the genus which has adapted to human settlement, and it is most common, almost weedy, in parts of the Constantia area of the Cape Peninsula where it thrives under the naturalized oaks and pines. Elsewhere it is found in open, sunny situations and always on a heavy soil, usually clay.

The nomenclatural history of *M. vegeta*, the type species of the genus, is complex. Until recently the species was known as *M. juncea* L. (Brown, 1928), but

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[6] *Moraea vegeta* in Miller's sense (Gard. Dict. ed. 8. 1768.) refers to *Dietes* (*Moraea*) *iridioides* (L.) Sweet ex Klatt; similarly *D. vegeta* sensu N. E. Brown refers to *D. iridioides* (see Barnard & Goldblatt, 1975).

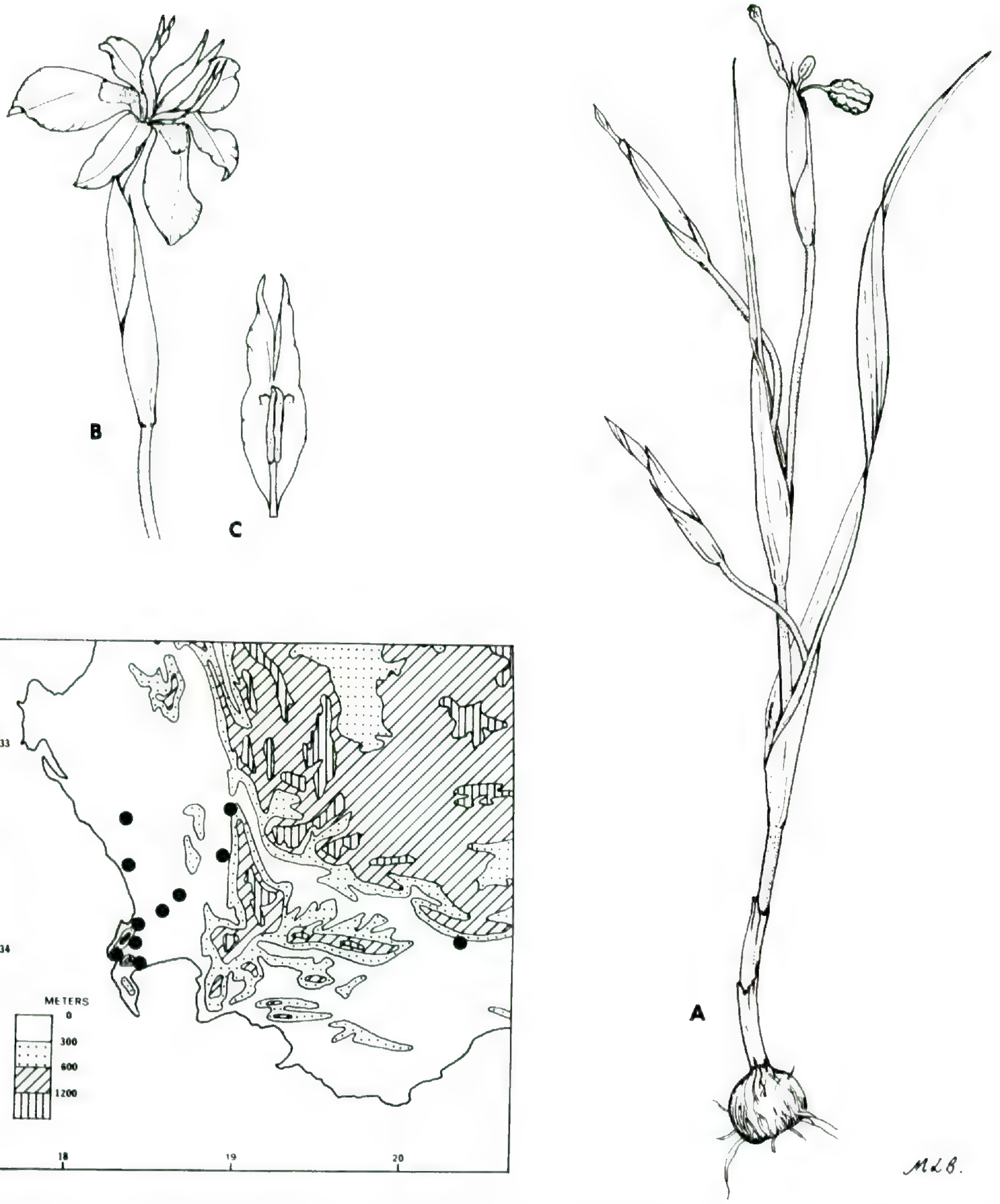


FIGURE 8. Morphology and distribution of *Moraea vegeta*.—A. Habit (×0.3).—B. Flower (life size).—C. Style branch and stamen (×2).

this has been shown to be a nomen nudum (Barnard & Goldblatt, 1975) which cannot be identified. *Moraea vegeta* was first mentioned together with *M. juncea* by Linnaeus in 1762 where short diagnoses with incomplete reference to Miller's *Figures of Plants* were given. Subsequently in 1767, Linnaeus cited Miller's *Figures of Plants, Tab. 237, fig. 2* in referring to *M. vegeta* but did not elaborate on *M. juncea*, which remains to this day something of a mystery. This relatively simple situation became confused when the eighth edition of Miller's *The Gardeners Dictionary* misapplied *M. vegeta* to the following plate, *Tab. 238, fig. 1*,

a species already described by Linnaeus as *M. iridioides* (now the type species of *Dietes*), while naming the type illustration of *M. vegeta*, *Tab. 237*, *M. juncea*. Although this error was noted and corrected in subsequent editions, it provided Brown with the idea that the correct name of the type species of *Moraea* might be *M. juncea*. Following Brown's published work on the subject, *M. juncea* was cited as the "conserved type" of *Moraea*. This error, only recently exposed fully (Barnard & Goldblatt, 1975) resulted in the name *M. vegeta* being applied to *Dietes*, as *D. vegeta* (L.) N. E. Brown subsequent to 1928.

Before N. E. Brown's treatment the name *Moraea tristis* (L.f.) Ker was used for *M. vegeta*, even when the earlier synonym was known (Ker, 1803).

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Near Darling (AD), *Lewis Grant & Theiler 4609* (BOL). Mud River turn-off, Darling road, *Goldblatt 307* (BOL). Lions Head, Cape Town (CD), *H. Bolus s.n.* (BOL). Camp Ground, Cape Peninsula, *Wolley Dod 597* (BOL, K). Sherwood, Kenilworth, *H. Bolus s.n.* (BOL). Claremont, Cape Peninsula, *Stokoe s.n.* (SAM-54345). Salt River, Cape Town, *Zeyher 72* (SAM, PRE). Wellington (DB), *Lewis Grant 2307* (BOL, MO). Durbanville (DC), *Barker 820* (NBG). Phesante Kraal, *Compton 16012*. (BOL, NBG).

33.19 (Worcester): Nuwe Kloof (AC), *Schlechter 9018, 2549* (K, PRE).

33.20 (Montagu): Swellendam Mountains (CD), *Marloth 8647* (PRE).

34.18 (Simonstown): Groot Constantia, Cape Peninsula (AB), *Goldblatt 474* (BOL). Constantiaberg, *MacOwan s.n.* (SAM-20576).

4. **Moraea indecora** Goldbl., sp. nov. TYPE: South Africa, Cape, sandy flats, 8 km E of Nababeep, *Goldblatt 3053* (MO, holotype; NBG, PRE, S, isotypes). —FIG. 9.

Planta magna, caule ramosa. *Cormus* ad 3 cm latus, profunde infossus, tunicis fibrosis. *Folia* 3–6, inserta supra terram. *Flores* lutei; tepala exteriora 2.5–4 cm longa, effusa, unguis brevis, ad 5 cm longis; tepala interiora 3–3.5 cm longa, effusa. *Filamenta* ca. 8 mm longa, connata ad base; *antherae* 8–10 mm longa, stigmata excedentes. *Capsula* ca. 1.5 cm longa, subpendula; *semina* orbiculata ad angulata.

Plants large, 35–60 cm high. *Corm* very deep seated, to 25 cm below the surface, ca. 2 cm in diameter; tunics of fine fibers. *Leaves* 3–6, inserted well above ground level, exceeding the inflorescence, ca. 1 cm wide, canaliculate. *Stem* leafless for 10–15 cm above ground, much branched. *Spathes* herbaceous below, dry above, with dark brown apices; inner spathes 4–5 cm long, the outer about 3–4 cm. *Flower* large, yellow; outer tepals 2.5–4 cm long, lanceolate, spreading, the claw short, ca. 5 mm long; inner tepals 2.2–3.5 cm long, also spreading. *Filaments* ca. 8 mm long, joined only near the base; *anthers* 8–10 mm long, exceeding the stigma, the pollen bright red. *Style* ca. 1.2 cm long, the crests 7–15 mm long. *Capsules* 1.5 cm long, 8 mm wide, showing impression of the seeds, subpendulous. Chromosome number $2n = 16$ (*Goldblatt 3053*, type collection).

Flowering time: October.

Distribution: Deep sandy soil, in central Namaquland around Springbok.—FIG. 9.

Moraea indecora was only recently discovered while I was studying *Moraea* in Namaqualand in the spring of 1974. During mid-October, after a season of particularly good, though late rains, this species was found at two sites, one north of Springbok near Nababeep and the other west of Springbok on the road

FIGURE 9. Morphology and distribution of *Moraea indecora*.—A. Habit (×0.25).—B. Corm (× 0.5).—C. Flower (life size).—D. Style branch and stamen (× 1.5).

to Spektakelberg. It grows in the typical coarse, granite-derived sand of Namaqualand, in level, open areas and was found together with the recently described *M. margaretae*, a similar though much smaller species. The two may perhaps be confused, although size alone distinguishes them. *Moraea indecora* is peculiar in having the lowermost leaves inserted well above the ground, just below the first branch. This, together with the large yellow flowers, bright red anthers which extend beyond the stigmas, and subpendulous capsules leave no doubt about the validity of this species. The large corms of *M. indecora* are particularly deep seated, being at least 20 cm below the surface, partly wedged in bed rock.

This species clearly belongs in section *Moraea* and is probably most closely related to *M. vegeta* and perhaps *M. margaretae*. It shares with the former a similar subpendulous capsule and rather fibrous corm tunics. Though similar in general appearance to *M. margaretae*, it differs in several aspects such as branching and flower structure, as well as overall size.

The chromosome number of $n = 8$ in *Moraea indecora*, reported here for the first time, is unusual in subgenus *Moraea* where $n = 10$ predominates and only a few aneuploid species are known, such as *M. papilionacea* and *M. tricolor* ($n = 9$) and *M. fugax* ($n = 8$ and 6). In spite of its lower chromosome number, there is good reason for including *M. indecora* in section *Moraea* where its many leaves and branched habit are quite consistent with the general morphological pattern.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Sandy flats, 8 km E of Nababeep (DB), *Goldblatt 3053* (MO, NBG, PRE), *3062* (MO, NBG). W of Springbok on road to Spektakelberg, *Goldblatt 3060* (K, MO, NBG, PRE).

5. **Moraea fergusoniae** L. Bol., S. African Gard. 19: 294. 1929. TYPE: South Africa, Cape, Riversdale, *Ferguson s.n.* (BOL-18970, holotype).—FIG. 10A–B.

M. fimbriata Klatt, Linnaea 34: 561. 1866; Baker, Fl. Cap. 6: 13. 1896, nom. illeg., non Loisel., 1822. TYPE: South Africa, Cape, Caledon, *Ecklon & Zeyher Irid. no. 42* (SAM, lectotype).

Plants 10–20 cm high, simple or usually 2–4-branched from the base. *Corm* 5–15 mm in diameter; tunics of pale medium fibers. *Leaves* 3–6, to 1 cm wide, seldom exceeding 10 cm long, dark green, usually glabrous, falcate or loosely coiled, the margins ciliate, undulate to crisped. *Stem* terete, glabrous, consisting of a few short internodes near the ground and 1 long upper internode, branching only near ground level. *Spathes* herbaceous with brown, attenuate apices; inner spathe 2.6–3.8 cm long, the outer ca. half the inner. Flowers white to cream, rarely blue with a yellow nectar guide; outer tepals to 2 cm long, lanceolate, the limb ca. 1.1 cm long; inner tepals erect, 8–12 mm long, entire and narrowly lanceolate or with a long central cusp and 2 small lateral lobes near the midline. *Filaments* to 4 mm long, entirely united or free for the upper 1 mm; *anthers* 3 mm long, yellow. *Style branches* 3–5 mm long, the crests linear, 5–7 mm long. *Capsule* ca. 7 mm long, clavate; seeds angled. Chromosome number $2n = 20$.

Flowering time: Late July and August.

FIGURE 10. *Moraea* species.—A–B. *Moraea fergusoniae*.—A. Habit (×0.5).—B. Flower (life size).—C–D. *M. margaretae*.—C. Habit (×0.75).—D. Flower (life size).—E–F. *M. papilionacea*.—E. Habit (×0.75).—F. Flower (life size).

Distribution: Clay slopes and flats from the Caledon district eastwards to Robinson Pass near Mossel Bay.—FIG. 11.

Moraea fergusoniae is very closely allied to *M. papilionacea* from which it is best distinguished by its white to ivory or blue flower that sometimes has tricuspidate inner tepals, a glabrous stem, and twisted leaves with undulate to crisped mar-

gins. It occurs on clay flats and slopes in the southern Cape between Botrivier in the Caledon district and the Langeberg foothills near Mossel Bay.

Though originally described as *M. fimbriata* by Klatt from an Ecklon and Zeyher collection from Caledon, this epithet, unfortunately a homonym of *M. fimbriata* Loisel (a synonym for *Iris cristata* Soland.), must be rejected. The correct name for this species, *M. fergusoniae*, was provided by Louisa Bolus who was apparently unaware that this was conspecific with Klatt's species.

SOUTH AFRICA. CAPE: 33.22 (Oudtshoorn): Robinson Pass (CC), *Hiemstra s.n.* (MO).
34.19 (Caledon): Slopes north of Botrivier (AA), *Bolus 9926* (BOL, K). Caledon Baths (AB), *Guthrie 2520* (BOL, NBG). Near Caledon, *Ecklon & Zeyher s.n.* (PRE, MO, SAM), *Ecklon & Zeyher Irid. no. 42* (SAM); *Stayner s.n.* (NBG-88048). Kleinriviersberge (AD), *Ecklon & Zeyher 4091* (C, K, PRE, S). Genadendal (BA), *Pappe s.n.* (K). Fairfield (BD), *Barnard s.n.* (SAM-68453).
34.20 (Bredasdorp): Bontebok Park, Bredasdorp (CA), *Acocks 22519* (PRE). The Poort, Bredasdorp, *Barker 2524* (BOL, NBG).
34.21 (Riversdale): Riversdale (AB), *Ferguson s.n.* (BOL-18970); *Muir 4874* (K).

6. **Moraea papilionacea** (L.f.) Ker, Bot. Mag. *tab. 750.* 1804; Baker, Fl. Cap. 6: 12. 1896.—FIG. 10E–F.

Iris papilionacea L.f., Suppl. Pl. 98. 1781. TYPE: South Africa, Cape, hills near Cape Town, *Thunberg s.n.* (Herb. Thunberg 1145, UPS, lectotype).
Moraea pilosa Wendl., Bot. Beob. 42. 1798. TYPE: unknown.
Iris hirsuta Licht. ex R. & S., Syst. Veg. 1: 478. 1817. TYPE: unknown, collected in the Tulbagh district.
Moraea hirsuta (Licht. ex R. & S.) Ker, Irid. Gen. 43. 1827.
Vieusseuxia intermedia Eckl., Top. Verz. 12. 1827, nom. nud.
V. nervosa Eckl., Top. Verz. 12. 1827, nom. nud.
Moraea papilionacea var. *maythamiae* Lewis, J. S. African Bot. 37. 1949. TYPE: South Africa, Cape, Rondebosch Common, *Salter 8989* (SAM, lectotype; BOL, NBG, isolectotypes).

Plants 10–15 cm high, simple to 5-branched. *Corm* 5–15 mm in diameter; tunics brown to black, the fibers medium to coarse. *Leaves* 2–4, linear, to 7 mm wide, occasionally exceeding the inflorescence, falcate, lightly pubescent on the abaxial surface, occasionally glabrous, the margins sparsely ciliate. *Stem* terete, lightly puberulous to villous, 1–2 internodes long, branching at the base or from the upper node. *Spathes* herbaceous, often with dry brown apices, pubescent or occasionally glabrous; inner spathe 3–6 cm long, the outer ⅓–⅔ the length of the inner. *Flowers* few per spathe, yellow or salmon colored, the nectar guides outlined in green or red, sweetly scented; outer tepals ca. 2.5 cm long, to 5 mm wide, outspread. *Filaments* 3–6 mm long, united at the base only; *anthers* ca. 4 mm long, the pollen red. *Style branches* to 8 mm, the crests lanceolate, 1–1.5 cm long. *Capsule* broadly ovate, 7–8 mm long, ca. 5 mm wide; *seeds* angular. Chromosome number $2n = 18$.

Flowering time: August to October.

Distribution: Flats and slopes; in clay or sand, usually poorly drained areas, from the Cedarberg in the north to the Caledon district.—FIG. 11.

Moraea papilionacea is readily distinguished from its allies by its brick red to yellow flower, pubescent stem, and leaf which is either villous on the margins and veins or at least ciliate on the margins. Its closest relative, *M. fergusoniae*, with white to blue flowers, has a glabrous stem though the leaves have ciliate

margins; *M. margaretae*, also closely related, has glabrous stems and leaves which have minutely ciliate leaf margins; *M. vegeta*, a more distant ally, has a puberulous stem but smooth leaf margins. *Moraea papilionacea* appears to be replaced from the Caledon district eastwards by *M. fergusoniae*. Though both occupy a similar habitat, growing in clay soil amongst low ericoid shrubs, and both occur in the Caledon district, they have not been reported growing together. *Moraea papilionacea* with $n = 9$ is clearly an aneuploid species, this number being derived from the basic $x = 10$ in subgenus *Moraea*.

Two species, *Moraea pilosa* and *M. hirsuta* are included in the synonymy; these are known only from description and the types are evidently lost. The identities of the two Ecklon nomina nuda included in the synonymy are known from annotations on Ecklon and Zeyher collections at the Riksmuseum at Stockholm, and elsewhere.

Moraea papilionacea has a somewhat limited range, from the central Cedarberg, above Algeria where a dwarf form occurs, south to the Caledon district. It is variable and four forms can be distinguished. The commonest and best known is the large salmon or yellow form found on clay flats and slopes between the Cape Peninsula and the Tulbagh area; east of the Hottentots Holland and Kogelberg ranges, near Caledon and Hermanus, clear yellow, glabrous-leafed plants are found; while to the north of the Tulbagh area in the Cedarberg and Cold Bokkeveld ranges a very diminutive slender-leafed form is found on sandy soils. A last form, found on sandy soils in the Cape Peninsula and surrounding Cape Flats, was given varietal rank by G. J. Lewis as var. *maythamiae*; this has a slender leaf, is almost glabrous, and, according to Lewis, blooms in late afternoon, whereas other forms flower from midmorning. The variety is not recognized as plants intermediate between it and the commoner typical variety are known. Also, since none of the other recognizable forms of *M. papilionacea* are accorded taxonomic status, it would be inconsistent to accept var. *maythamiae*.

SOUTH AFRICA. CAPE: 32.19 (Wuppertal): Elandskloof (CA), *Lewis s.n.* (BOL). Warm Baths, Olifants River valley, *Edward s.n.* (BOL-14436).

33.18 (Cape Town): Basons farm, Darling (AD), *Barker 6766* (NBG). Darling road, Ganzekraal turnoff, *Barker 719* (NBG). Near Darling, *Bolus 12831* (BOL, BR, PRE). Lower slopes, Devils Peak (CD), *Wolley Dod 596* (BOL); *Ecklon 818* (K, PRE); *Froembling s.n.* (NBG); *Treleaven 98* (SAM). Camp Ground, Cape Peninsula, *Ecklon & Zeyher 5021* (SAM). *Salter 8989* (NBG), *9643* (BOL, PRE, SAM). Cape Town, *Marloth 193* (PRE); *Prior s.n.* (PRE). Dal Josafat (DA), *Middlemost s.n.* (NBG-58644); *Lewis Grant 2347* (BOL, BR, K, M, MO); Near Durbanville (DC), *Esterhuysen 17505* (BOL, PRE). Bottelary road, Stellenbosch (DD), *Lewis 2228, 2229* (both SAM). Jonkershoek valley, *Lewis 1652* (SAM).

33.19 (Worcester): Near Tulbagh Road Station (AC), *Goldblatt 193* (BOL). Between Bains Kloof and Wolseley, *Goldblatt 2430* (MO). Prince Alfreds Hamlet (AD), *Walgate 384* (NBG). Gydo, *Leipoldt 4080* (BOL). Bothas Halt (CA), *Gillet 243* (BOL).

34.18 (Simonstown): Steenberg, Cape Peninsula (AB), *Compton 13640* (NBG). Kloof Nek (Hout Bay Nek), *Schlechter 1310* (K, S, SAM); *Goldblatt 445* (BOL); *Pillans 10690* (MO). Faure (BA), *Strey 558* (PRE); *Compton 16242* (NBG). Flats between Gordon's Bay and Strand, *Esterhuysen 23129* (BOL).

34.19 (Caledon): Elgin (AA), *Dahlstrand 1182* (PRE). Caledon commonage (AB), *Barker 118* (BOL, K). Zwartberg, *Ecklon & Zeyher s.n.* (PRE-22396, S). Vogelklip, Hermanus (AD), *Barker 1787* (NBG). Between Caledon and Shaws Pass, *Goldblatt 301* (BOL).

Without precise locality: Near Ceres, *Marloth 147, 12994* (both PRE). Cedarberg, *Thode A2075* (PRE). Cape of Good Hope, *Sparrman s.n.* (S); *Thunberg s.n.* (S).

7. **Moraea margaretae** Goldbl., Ann. Missouri Bot. Gard. 63: 19. 1976. TYPE: South Africa, Cape, Namaqualand, pipeline track, SW of Nababeep, *Goldblatt 628* (BOL, holotype; K, MO, PRE, S, isotypes).—FIG. 10C–D.

Plants to 15 cm high, usually 1–2-branched. *Corm* 5–7 mm in diameter; tunics brown, coarsely fibrous, the inner layers entire. *Leaves* 2–3, linear, canaliculate, often terete and twisted near the apex. *Stem* glabrous, usually branching from the base. *Spathes* herbaceous, with dark brown, acute or lacerated apices; inner spathe 3–4.5 cm long, the outer 2–3 cm long. *Flowers* few, pale yellow; outer tepals 2–3 cm long, the limb 1.5–2 cm long, spreading to reflexed; inner tepals erect, spreading later, lanceolate, obtuse, to 2.0 cm long. *Filaments* ca. 5 mm long, joined for 4 mm; *anthers* 4–5 mm, red. *Style branches* ca. 7 mm long, the lanceolate crests 6–10 mm long. *Capsule* and *seeds* unknown. Chromosome number $2n = 40$.

Flowering time: Late September and October.

Distribution: Coarse sandy soils in Namaqualand.—FIG. 11.

Moraea margaretae is closely related to *M. papilionacea*, a common southwestern Cape species. The two can readily be distinguished by the stem which is lightly villous in *M. papilionacea* but entirely glabrous in *M. margaretae*. The flower and habit of *M. margaretae* is similar to the newly discovered *M. indecora*, but the two differ in several details (see discussion under *M. indecora*).

Though rather poorly collected, I have found *M. margaretae* to be quite common from Garies north to Springbok. It grows in sandy soils, in both hilly and flat places. It is rather late flowering, usually after the end of the flowering period of most Namaqualand plants, and this may explain why it is so rarely collected. *Moraea margaretae* is evidently a polyploid species, with two reports of $2n = 40$, the only recorded polyploid in section *Moraea*.

SOUTH AFRICA. CAPE: 29.17 (Springbok): 4 km W of Steinkopf (BA), *Goldblatt 2775* (MO). Koufontein, Steinkopf district (BC), *Herre s.n.* (STE-11835). Pipeline road S of Nababeep (CA), *Goldblatt 628* (BOL, K, MO, PRE, S). 8 km E of Nababeep (CB), *Goldblatt 3061* (NBG, MO, PRE).

30.17 (Hondeklipbaai): 8 km N of Garies (BD), *Leighton 1129* (BOL). Brackdam, hills, *Schlechter 11120* (BM).

Without precise locality: Namaqualand minor, *Scully 134* (BM).

8. **Moraea serpentina** Baker, Handbook Irid. 52. 1892. TYPE: South Africa, Cape, Okiep, stony places, *Bolus 6572* (K, lectotype; GRA, isolectotype). Little Namaqualand, *Bolus 6571* (BOL, K syntypes); Ezelskop-Roodeberg, Khamiesberg, *Drège 2599* (K, S, syntypes).—FIG. 12A–B.

M. arenaria Baker, Handbook Irid. 52. 1892. TYPE: South Africa, Cape, sandhills, Ebenezer, *Drège 8324* (K, holotype; S, isotype).

M. framesii L. Bolus, S. African Gard. 17: 418. 1927. TYPE: South Africa, Cape, near Calvinia, *Ross Frames s.n.* (BOL, holotype).

Plants 4–20 cm high, usually branched. *Corm* 8–20 mm in diameter, asymmetric at the base; tunics of tough coarse, usually dark fibers. *Leaves* basal only, or occasionally cauline, (1–)3(–5), rarely solitary, canaliculate or ± flat, undulate-flexuose, glabrous or lightly pubescent on the margins or on the abaxial surface. *Stem* 2–3 internodes long, branching from the base or the upper nodes. *Spathes*

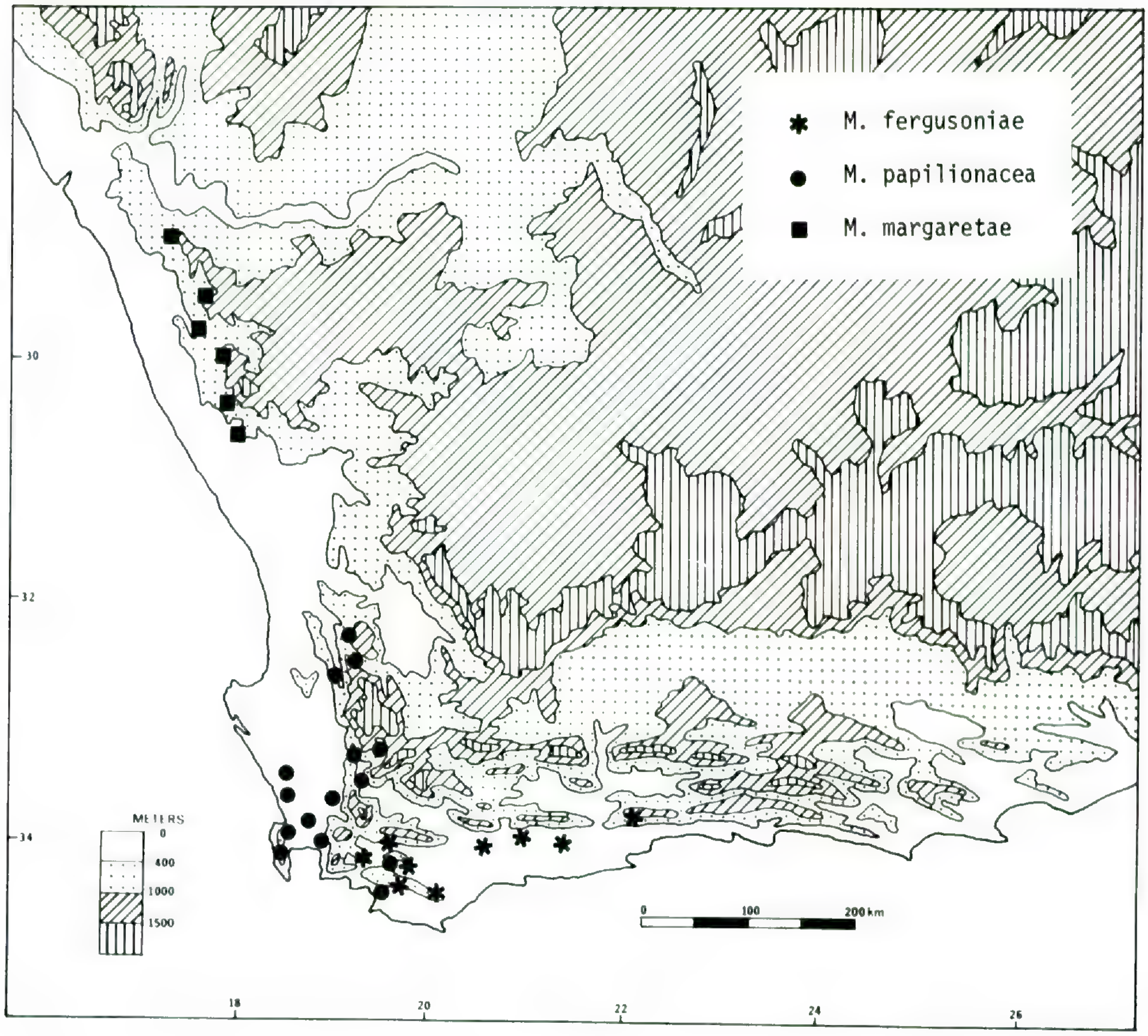


FIGURE 11. Distribution of *Moraea fergusoniae*, *M. papilionacea*, and *M. margaretae*.

usually dry, membranous, the apices entire, attenuate, or often lacerated; inner spathe 1.5–3 cm long, the outer ± half the inner. *Flowers* few per spathe, white to yellow, sometimes flushed with mauve or pink, the nectar guides large and yellow; outer tepals 2.4–3.0 cm long, the claw to 1 cm long, the limb 1.5–2.5 cm wide, obtuse-retuse; inner tepals 2–3 cm long, erect, broadest near the apex. *Filaments* 5–7 mm long, joined near the base only or to midline; *anthers* 3–5 mm long. *Style branches* ca. 6 mm long, the crests 4–8 mm, lanceolate. *Capsule* enclosed in the spathes, clavate, ca. 1 cm long; *seeds* angled. Chromosome number $2n = 20$.

Flowering time: September to October.

Distribution: Sandy to gravelly places, extending along the west coast from Klawer in the south to the Richtersveld in the north, also occurring in Bushmanland and the Karoo.—FIG. 13.

When Baker (1892) described *Moraea serpentina* and *M. arenaria*, here treated as conspecific, he distinguished them by their leaves. While both had more or less twisted, coiled leaves, *M. serpentina* was described as having a pilose,

FIGURE 12. *Moraea* species.—A–B. *M. serpentina*.—A. Habit (×0.75).—B. Flower (life size).—C–D. *M. tortilis*.—C. Whole plant (×0.75).—D. Style branch and stamen (×1.5).

very flexuose, linear leaf, and *M. arenaria* as having a spirally twisted, glabrous, ± terete leaf. Examination of type material, however, reveals that *M. arenaria* does not have a truly terete leaf, rather it is of the same type as *M. serpentina*, only narrower but distinctly bifacial and channeled. It is glabrous, but this is a poor distinguishing character, for among the three collections of *M. serpentina* cited by Baker, only one, *Drège 2599*, from the Khamiesberg is clearly pilose. In fact, examination of many wild populations of this species from Namaqualand reveals that the pilose leaf occurs occasionally in several areas in forms with a bifacial leaf. It is commonest in the Khamiesberg but is also found near Okiep and Steinkopf. When the variation in leaf form is taken into account, *M. serpentina* and *M. arenaria* cannot be regarded as separate species.

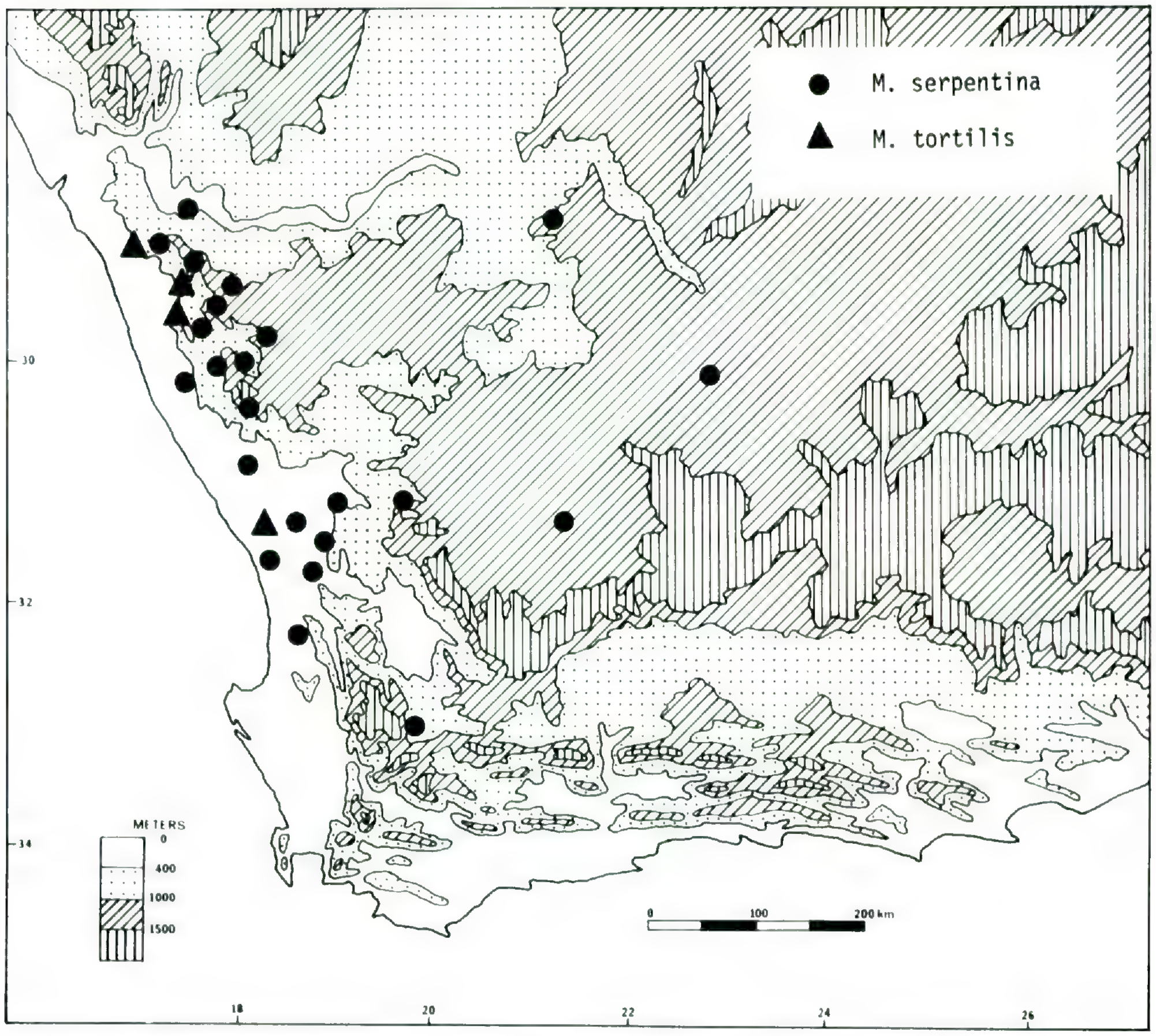


FIGURE 13. Distribution of *Moraea serpentina* and *M. tortilis*.

Moraea framesii, clearly simply a glabrous-leafed form of *M. serpentina* with a broader than typical leaf, is also included in synonymy here.

Moraea serpentina, especially under its synonym *M. arenaria*, has often been associated with a second species described in this paper, *M. tortilis*, which has a truly terete, spirally coiled leaf. Vegetatively the species are similar, except for the quite terete leaf, and may occasionally be confused. The flowers are, however, quite distinct. *M. serpentina* has a white flower often flushed purple or pink, with large nectar guides and erect inner tepals, while *M. tortilis* has white to dark blue flowers with smaller nectar guides and broad reflexed inner tepals. These very significant floral differences are often quite obscured in dried material so that the leaf must be used for distinguishing these two taxa.

Moraea serpentina is very common in dry areas of the Van Rynsdorp district and extends north to Springbok. It usually blooms quite late, in October, but has been collected in flower from the end of August. The handful of records to the east of Namaqualand in Bushmanland and the Karoo may indicate a scattered distribution here, but it is equally likely that these areas are simply rather poorly collected.

South Africa. cape: 28.17 (Vioolsdrif): Stinkfontein (CD), *Schlechter 11091* (BOL, BR, GRA, K, PRE, S).

28.21 (Upington): Klipkoppies, between Upington and Kenhardt (CD), *Lewis 249* (SAM).

29.17 (Springbok): Ca. 10 km W of Steinkopf (BA), *Strauss 139* (NBG). Anenous flats, *Marloth 12215* (BOL, PRE). Near Springbok (DB), *Lewis 740, 741* (SAM). Near Okiep, *H. Bolus 6572* (BOL, K); *O'Connor Fenton s.n.* (BOL). Near Concordia, *L. Bolus s.n.* (BOL); *Lewis 5533* (NBG). Hills E of Nababeep, *Goldblatt 630* (BOL); *Goldblatt 3051* (MO, PRE). Mesklip (DD), *Compton 5419* (BOL); *Schlechter 11284* (BR, K, MO, S). Ca. 18 km SW of Springbok, *Acocks 19570* (K, NBG, M, PRE). Droedap, *Esterhuysen 5892* (BOL, K, PRE); *Compton 11443* (NBG).

29.18 (Gamoep): 40 km E of Springbok (CA), *Salter 3789* (BOL).

30.17 (Hondeklipbaai): Soebatsfontein (BA), *Barker 6700* (NBG). Between Buffels River and Soebatsfontein, *Leighton 1210* (BOL); *Lewis 1634* (SAM).

30.18 (Khamiesberg): Between Roodeberg and Ezelskop (AC), *Drège 2599* (K, S). Khoms Ravine, *Pearson 6651* (BOL, K). Foot of Studers Pass, *Goldblatt 634* (BOL). Khamiesberg, *Compton 13222* (NBG). 10 km NNW of Bitterfontein (CC), *Acocks 19507* (K, NBG).

30.23 (Britstown): Smartts Syndicate between Prieska and Britstown (CB), *Marloth s.n.* (BOL).

31.18 (Van Rhynsdorp): Near Bitterfontein (AA), *Lewis Grant 4776* (MO). Knechtsvlakte (BC), *Pillans 6336* (BOL, K). Ebenezer, sandhills (CA), *Drège 8324* (K). Van Rhynsdorp (DA), *Barker 5876* (NBG). Wiedouw River, *Lewis 2324* (SAM); *Goldblatt 3075A* (MO).

31.19 (Calvinia): Near Blaaukrans, 55 km NW of Calvinia (AB), *Lewis 2753* (SAM). Kliprand turnoff, Nieuwoudtville-Loeriesfontein road (AC), *Goldblatt 578* (BOL). Brandkop, between Nieuwoudtville and Loeriesfontein, *Stokoe s.n.* (SAM-55646). Foot of Van Rhyns Pass, *L. Bolus s.n.* (BOL-19359, BM, K); *Goldblatt 270* (BOL); *Loubser 950* (NBG); *Hall 3361* (NBG).

31.20 (Williston): 25 km W of Williston, arid karoo (BD), *Acocks 17709* (K, M, NBG, PRE).

32.18 (Clanwilliam): Graafwater (BA), *Zinn s.n.* (SAM-59815).

33.19 (Worcester): Karoo Poort (BB), *Herre s.n.* (BOL).

9. **Moraea tortilis** Goldbl., sp. nov. type: South Africa, Cape, quartzite slopes between Okiep and Steinkopf, *Goldblatt 2771* (MO, holotype; K, NBG, PRE, isotypes).—Fig. 12 C–D.

Planta 10–15 cm alta, saepe pauciramosa. *Tunicae* cormis atrobrunneae fibris crassis. *Folia* (1–)–3, teretia, glabra, helicoidea. *Flores* coerulei ad albi; tepala omnia reflexa ad 45°; tepala exteriora 2.5–3.5 cm longa; tepala interiora breviora. *Capsula* clavata, ad 1.3 cm longa; *semina* parva, angulata.

Plants 10–15 cm high, usually branched. *Corm* ca. 10 mm diameter, asymmetric at the base; tunics of tough, dark fibers. *Leaves* basal and sometimes cauline, (1–)2–3, terete (becoming flattened adaxially when dry) and coiled helically like a corkscrew, glabrous. *Stem* 2–3 internodes long, branching from the base and upper nodes. *Spathes* herbaceous below, becoming completely dry and lacerated; inner spathe 2.5–4 cm long, the outer ± half the inner. *Flowers* blue to white with a small yellow nectar guide; outer tepals 2.5–3.5 cm long, the claw to 1.4 cm long, the limb ca. 2 cm wide, obtuse-retuse; inner tepals to 3 cm long, reflexed to 45°. *Filaments* 8 mm long, joined in the lower half; *anthers* 5 mm long. *Style branches* to 1 cm long, the crests narrow, ca. 1 cm. *Capsule* clavate-oblong, to 1.3 cm long; *seeds* angled. Chromosome number $2n = 20$ (*Goldblatt 2771*, type collection).

Flowering time: September to October.

Distribution: Sandy to stony places, frequently associated with quartzite, occurring locally along the west coast from Klawer to Steinkopf, Namaqualand.—FIG. 13.

This beautiful species has been known for many years and though collected occasionally, it was associated with *Moraea arenaria* Baker. It has become clear through the examination of living plants that *M. serpentina* and *M. arenaria* are conspecific with *M. framesii*, and the allied *M. tortilis* is distinct.

Moraea tortilis is closely related to *M. serpentina*, but when fresh flowers are examined the differences become very obvious. The blue or white flowers of *M. tortilis* have reflexed inner tepals and small nectar guides in marked contrast to the flowers of *M. serpentina* which have large yellow nectar guides and invariably erect inner tepals. The vegetative aspect of the two species is similar, but the leaves of *M. tortilis* are terete when fresh and coiled like a corkscrew, while those of *M. serpentina* are channeled or flat, though often very narrow, and are usually laxly undulate and twisted, though sometimes coiled as in *M. tortilis*.

Moraea tortilis and *M. serpentina* grow in the same general area of the Cape west coast from the Van Rhynsdorp district north to Steinkopf in Namaqualand, but *M. tortilis* is much rarer and more limited in its range. Their habitats are similar, but *M. tortilis* is often associated with local quartzite patches.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Flats at Anenous (BA), *Marloth 12215* (STE). Steyerkraal, between Ratelpoort and Okiep (BD), *Lewis 5516* (NBG, STE). Quartzite outcrop between Okiep and Steinkopf, *Goldblatt 2771* (MO, NBG, PRE, S), *3040* (MO, NBG, PRE, S). Pipeline road SW of Nababeep (DB), *Goldblatt 3049* (MO, PRE).

Without precise locality: Namaqualand, *Marloth 6984* (PRE).

10. **Moraea lugubris** (Salisb.) Goldbl., Ann. Missouri Bot. Gard. 63: 18. 1976.—FIG. 14.

Ferraria lugubris Salisb., Prodr. Stirp. 42. 1796, nom. nov. pro. *Iris plumaria* Thunb.
Moraea iriopetala L.f., Suppl. Pl. 100. 1781, as to plant intended, not to name; Baker, Fl. Cap. 6: 17. 1896.
Iris plumaria Thunb., Diss. Irid. no. 16. 1782, nom. illeg. TYPE: South Africa, below Devils Peak, near Cape Town, *Thunberg s.n.* (Herb. Thunb. 1153, UPS, lectotype).
Moraea plumaria (Thunb.) Ker, Ann. Bot. (König & Sims) 1: 240. 1805.
Vieusseuxia geniculata Eckl., Top. Verz. 12. 1827, nom. nud.
Moraea mira Klatt, Trans. S. African Philos. Soc. 3: 202. 1885; Baker, Fl. Cap. 6: 17. 1896. TYPE: Cape Caledon district, slopes of Zwartberg near the Baths, *Templeman s.n.* sub *MacOwan 2162* (K, S).

Plants 6–16 cm high, usually 2–4-branched. *Corm* small, but enclosed in large basketlike tunics, with cormlets produced round the base. *Leaves* 2, linear, glabrous, the lower basal, the upper produced well above the ground. *Stem* 2 internodes long, strongly flexed; all branches produced from the aerial node. *Spathes* herbaceous, pale green, sometimes with brown apices; inner spathe 3–5 cm long, the outer seldom more than half the inner. *Flowers* few, bright blue; outer tepals to 1.8 cm long, the claw short, ca. 5 mm long, reflexed to 45°; inner tepals to 1.6 cm long, also strongly reflexed. *Filaments* to 6 mm long, free at the apex only; *anthers* oblong, ca. 3 mm long, apiculate, red. *Style branches* plumose, the crests single with feathery outgrowths from the base. *Capsule* spherical-ovoid, 6–8 mm long; *seeds* angled. Chromosome number $2n = 20$.

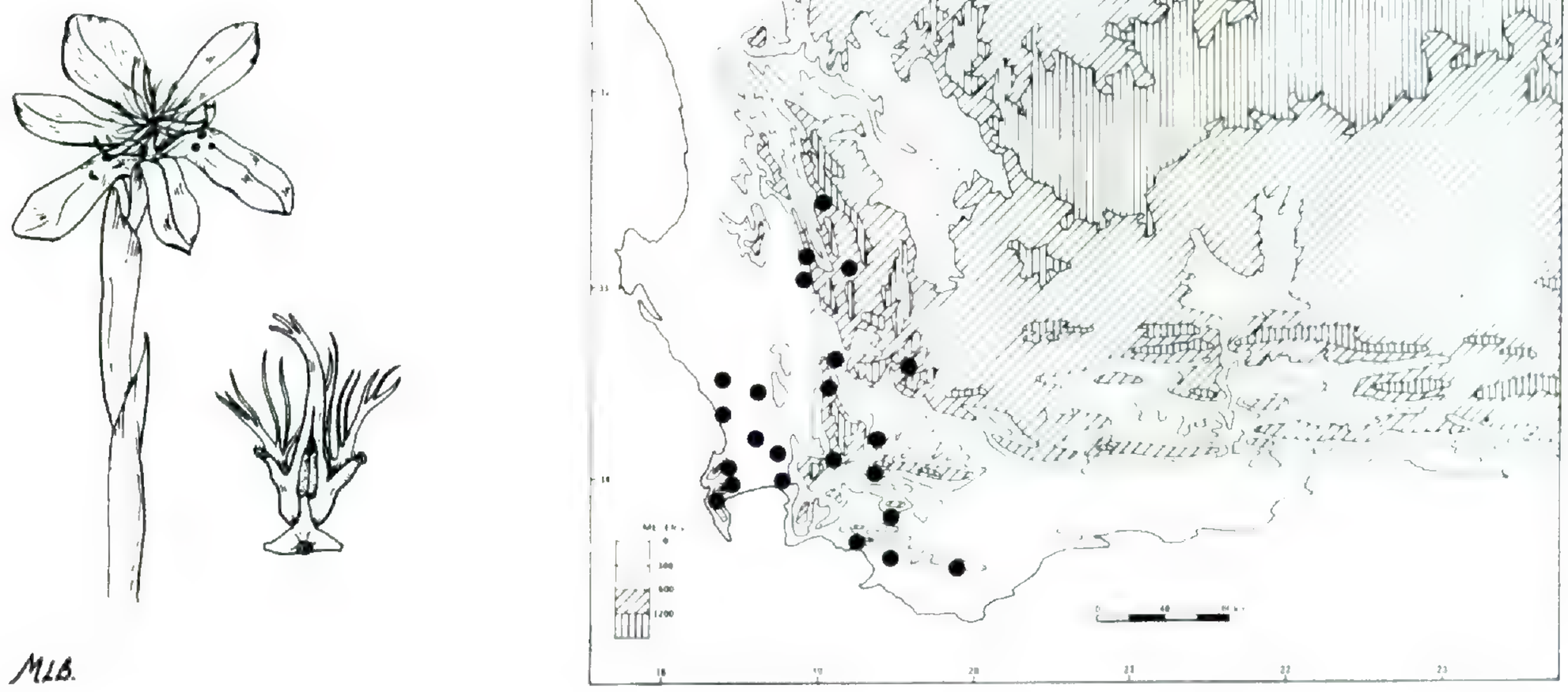


FIGURE 14. *Moraea lugubris*: distribution and flower (life size) with style branch and stamen enlarged.

Flowering time: Late August to early November.

Distribution: Common from Bredasdorp, westwards to Cape Town, also found north to Nieuwoudtville, usually in sandy soils, in damp places.—FIG. 14.

Moraea lugubris is a rather isolated species within section *Moraea*. Though distinct in several characteristics, it is remarkable for its corm tunics which usually form a large open network round the tiny corm (a feature apparently not developed in some forms) and particularly for the plumose style branches. The style crests themselves are not paired as in other members of the genus, but are single and irregular in outline, and are obscured by feathery plumose outgrowths. The species is usually quite small, and though common, is easily overlooked. It is found from the Caledon district in the south, along the west coast to Nieuwoudtville. Though the record suggests it is not common north of the Olifants River Mountains, this may be due to it being overlooked in this area rather than a true reflection of its distribution.

Moraea lugubris has a long taxonomic history, beginning with its collection by Sparrman who sent it to Linnaeus in 1773. Nothing was apparently done with the specimen until after Linnaeus's death when the younger Linnaeus decided to call it *M. iriopetala*. The description in the *Supplementum Plantarum* is, however, in such a form as to make *M. iriopetala* a superfluous synonym for *M. vegeta* (Goldblatt, 1976a).

Thunberg also collected *M. lugubris* and gave it the name *Iris plumaria*. Again, owing to the citation by Thunberg of *M. vegeta* in the synonymy, the selected epithet became a superfluous synonym for *M. vegeta*. Before *Iris plumaria* was transferred to *Moraea* by Ker in 1805, in which genus it can be treated as a valid new name, Salisbury proposed the name *Ferraria lugubris*, citing both earlier illegitimate names, *M. iriopetala* and *I. plumaria*, and this name is the one now applied to this plant. Klatt's *Moraea mira* appears to be no

more than a later synonym since there is no indication that Klatt considered *M. mira* distinct from *M. lugubris*, then known as *M. plumaria*.

SOUTH AFRICA. CAPE: 31.19 (Calvinia): Grasberg, near Nieuwoudtville (AC), *Barker 9554* (NBG, PRE, STE). Nieuwoudtville, *Galpin 11141* (PRE).

32.19 (Wuppertal): Elands Kloof (CA), *Lewis s.n.* (BOL); *Barker 3119* (NBG). Mountain plateau above Porterville (CC), *Estherhuysen 16152* (BOL, NBG). Wabooms River, Cold Bokkerveld, *Hanekom 779* (K, PRE).

33.18 (Cape Town): Groenekloof (Mamre) (AD), *Zeyher s.n.* (SAM-70705). Near Porterville (BB), *Barker 8145* (NBG); *Steyn 586* (NBG). Near Malmesbury (BC), *L. Bolus s.n.* (BOL-20285). Near Gansekraal, Darling district (CA), *Barker 718* (NBG). Kirstenbosch, Window Stream (CD), *Esterhuysen 11838* (BOL). Near Claremont, Cape Peninsula, *H. Bolus 2833* (BOL, PRE). Camp Ground, Cape Peninsula, *Wolley Dod 861* (BOL, K). Botterberg near Philadelphia (DA), *Wasserfall 215* (NBG). Stellenbosch flats (DD), *Duthie s.n.* (BOL-15943); *Garside 265* (K). Bottelary hills, *Hafstrom & Acocks 320* (PRE, S).

33.19 (Worcester): Wolseley (Ceres Road) (AC), *Schlechter 8984* (BOL, GRA, K, MO, PRE, S). Hex River valley (BC), *Tyson 720* (SAM). Bothas Halt (CA), *Compton 18276* (NBG). Bains Kloof, *Lewis Grant 2356* (BOL). French Hoek Peak (CC), *Stokoe s.n.* (SAM-58744). Between Worcester and Villiersdorp, *Lewis 2972* (SAM); *Compton 22909* (NBG).

34.18 (Simonstown): Muizenberg plateau (AB), *Powers s.n.* (SAM-58963); *Lewis 1013* (SAM). Klawer valley, Cape Peninsula, *Lewis 20* (SAM). Bergvliet, *Salter 7642* (SAM). Olifantsbosch (AD), *Compton 23717* (NBG). Patrys Vlei, Cape Peninsula, *Wolley Dod 1496* (BOL, K). Cape Flats below Wynberg (BA), *Schlechter 1545* (GRA, K). Firgrove (BB), *Compton 13472* (NBG); *Leighton 249* (BOL).

34.19 (Caledon): 8 km SW of Villiersdorp (AA), *Story 3047* (PRE). Slopes of Zwartberg (AB), *Templeman* sub *MacOwan 2612* (K, S). Hermanus (AC), *H. Bolus 9829* (BOL). 3 km from Stanford, near vlei (AD), *Gillett 4447* (BOL, MO). Drayton siding, E of Caledon (BA), *Goldblatt 340* (BOL). The Poort, 12 km from Bredasdorp (DB), *Dymond s.n.* (BOL-21228).

Section 2. **Acaules** Baker [as subgenus *Eumoraea* (section) *Acaules*], Fl. Cap. 6: 9. 1896. TYPE: *Moraea ciliata* (L.f.) Ker.

Plants small, with stem entirely subterranean. *Leaves* 3 to several, basal, canaliculate, linear-ensiform, not distinct from the spathes. *Stem* simple, or branching below ground. *Spathes* not distinct from the leaves, usually only the innermost entirely sheathing. *Flowers* borne on contractile pedicels; tepals unguiculate, the inner whorl erect to spreading. *Capsules* retracted into the spathes after flowering, borne near ground level, clavate, soft walled; *seeds* angular. Basic chromosome numbers $x = 10, 9$.

Distribution: Species occur over the entire winter rainfall region as well as in marginal areas to the east and north; one species extends from the west coast through the central karoo to East Griqualand.

Section *Acaules* comprises four species, all with a similar reduced vegetative habit in which the stem is entirely subterranean. The inflorescences are borne at ground level and the flowers are raised on pedicels which contract after flowering so that the fruit develops within the spathes. The unspecialized flowers, which have large inner tepals, are fugaceous and last only for part of a day. The flowers are also very delicate and particularly difficult to preserve, usually deliquescing and sticking to drying paper. Important floral characters are thus often lost in herbarium material.

The many-leafed habit and basic chromosome number of $x = 10$ place section

Acaules firmly in subgenus *Moraea*, and it is probably derived from section *Moraea* in which similar karyotypes are found (Goldblatt, 1976a). The base number of $x = 9$ in certain forms of *Moraea tricolor* is clearly derived from the ancestral $x = 10$.

11. **Moraea falcifolia** Klatt, Abh. Naturf. Ges. Halle 15: 366. 1882; Baker, Fl. Cap. 6: 12. 1896. TYPE: South Africa, Cape, Hantam Mountain, *Meyer* (1869) (B, lectotype; S, isolectotype).

M. galaxioides Baker, Handbook Irid. 49. 1892. TYPE: South Africa, Transvaal, *Mrs. Barber* (1872) (K, holotype).

M. fasciculata Klatt, Abh. Naturf. Ges. Halle 15: 366. 1882. TYPE: South Africa, Cape, "Langevaley," *Drège 2600* (B, holotype; K, P, S, isotypes).

Galaxia peduncularis Beguinot, Malpighia 23: 211. 1909. TYPE: South Africa, Cape, "Langevaley," *Drège 2600* (B, holotype).

Plants small, to 5 cm high, forming a dense sessile rosette. *Corm* to 2 cm in diameter; tunics of coarse dark fibers, often bearing cormlets round the base. *Leaves* several, some indistinguishable from the inflorescence spathes, slender, canaliculate, to 10 cm long, linear, falcate or loosely coiled, the margins frequently undulate and crisped. *Stem* not produced above ground, usually branching to give rise to several inflorescences. *Spathes*, especially the outer, sheathing at the base only, with well-developed equitant apices and not clearly distinct from the leaves, the inner usually entirely sheathing, to 2.5 cm long with membranous margins. *Flowers* several, white to cream with yellow nectar guides outlined in purple; outer tepals 1.5–2.2 cm long, the limb 8–11 mm long, to 15 mm wide; inner tepals 1.3–2.0 cm long, spreading. *Filaments* to 6 mm long, joined in the lower half; *anthers* 3–4 mm long. *Style branches* ca. 8 mm long, the crests 5–8 mm long. *Capsule* spherical-ovoid, to 1 cm long; *seeds* globose to slightly angled. Chromosome number $2n = 20$.

Flowering time: May to August(–September).

Distribution: Widespread in karoid or semikaroid vegetation from the southwestern Cape to the western Transvaal.—FIG. 15.

Moraea falcifolia was treated as a summer rainfall area species (Goldblatt, 1973) and its range in the Karoo and dry regions of the northern Cape, as well as the Cape West Coast and Namaqualand, make it one of the few species of *Moraea* found in both summer and winter rainfall areas. The extreme eastern form, from the western Transvaal, recognized by Baker as *M. galaxioides*, grades without noticeable discontinuity into western Cape forms which include the types of *M. falcifolia* from the Calvinia district and *M. fasciculata* from Langvlei, on the west coast. I have found *M. falcifolia* to be much more common than the record indicates: the very fugaceous flowers are seldom seen and the small plants themselves are apparently often overlooked.

Moraea falcifolia is allied to the more common western Cape species, *M. ciliata*, and belongs in section *Acaules*, which is characterized by the absence of an aerial stem and a contractile pedicel which pulls the ovary down to ground level after flowering. Though *M. falcifolia* is quite distinct within section *Acaules*, it may occasionally be confused with other species. It is distinctive in having

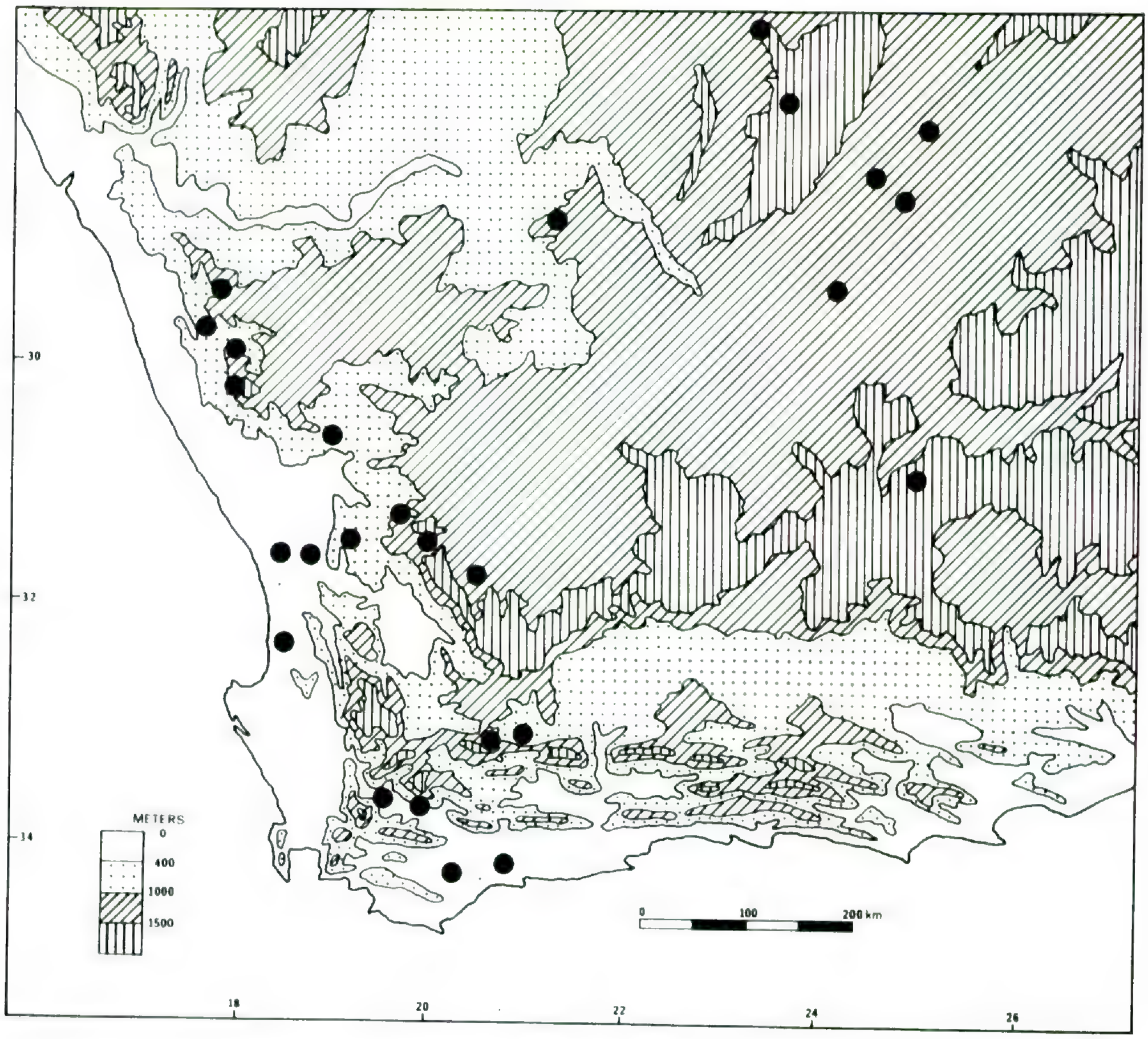


FIGURE 15. Distribution of *Moraea falcifolia*.

dark corm tunics and usually falcate, glabrous leaves that only rarely have a ciliate margin.

SOUTH AFRICA. CAPE: 27.23 (Kuruman): Baltharos (AD), *Silk 67* (BOL).
29.21 (Kenhardt): Jagbult, Kenhardt district (DA), *Acocks 12684* (K).
28.23 (Griekwastad): Danielskuil (BA), *Pole-Evans 98* (K, PRE); *Ekersohn 1339* (PRE).
28.24 (Kimberley): Witfontein, Barkly West, *Acocks 2482* (BOL, M, PRE). Diamond Fields, *Tuck s.n.* (K). Klip Drift, Vaal River (DA), *Barber s.n.* (K), *14*(K). Du Toit's Pan, *Tuck 13* (K).
29.17 (Springbok): Near Okiep (DB), *Foxwell s.n.* (K). Near Nababeep Wells, *Bolus 6578* (BOL). Concordia, *Schlechter 11343* (K, BM, BR, BOL, PRE). Mesklip (DD), *Compton 5410* (BOL, NBG).
29.24 (Hopetown): Newlands (AD), *Paton s.n.* (BOL-30838).
30.17 (Kamiesberg): Kamieskroon (BB), *Salter 868* (BOL).
30.19 (Loeriesfontein): 40 km N of Loeriesfontein (CB), *Hall 1385* (NBG).
31.18 (Van Rhynsdorp): Sandveld, Vredendal (CB), *Hall 4029* (BOL, NBG). Van Rhynsdorp (DA), *Salter 2506* (BOL). Foot of Giftberg, S of Van Rhynsdorp, *Goldblatt 636* (BOL).
31.19 (Calvinia): Glenlyon, Nieuwoudtville (AC), *Goldblatt 564* (BOL). Near Nieuwoudtville, *Salter 4551* (BOL); *Barker 9406* (NBG). Akkerdam, Calvinia (BC), *Lewis 5910* (NBG). Hantam Mountain, *Meyer 12* (B).

31.20 (Williston): Langfontein, SE of Calvinia (CA), *Hall 4254* (NBG).
31.24 (Hanover): 25 km NW of Naauwpoort (BA), *Acocks 14293* (PRE).
33.19 (Worcester): 15 km SW of Worcester (CA), *Stayner s.n.* (NBG-81696). Over Hex, *Morris 159* (NBG). Near Robertson (DD), *van Niekerk 583* (BOL).
33.20 (Montagu): Whitehill (BA), *Compton 3240* (BOL, NBG).
34.20 (Bredasdorp): Napky, Swellendam district (AB), *Acocks 22253* (PRE). Potteberg North (B), *Taylor 7198* (PRE).
Without precise locality: Transvaal, *Barber s.n.* (K).

12. **Moraea ciliata** (L.f.) Ker, Ann. Bot. (König & Sims) 1: 241. 1805. Baker, Fl. Cap. 6: 11. 1896, incl. vars.—Fig. 16.

Iris ciliata L.f., Suppl. Pl. 98. 1781. TYPE: South Africa, Cape, hills near Cape Town, *Thunberg s.n.* (Herb. Thunberg 1116, UPS, lectotype).
Moraea hantamensis Klatt, Abh. Naturf. Ges. Halle 15: 365. 1882. TYPE: South Africa, Cape, Hantam Mountain, *Meyer s.n.* (B).
M. macrochlamys Baker, Handbook Irid. 49. 1892. TYPE: South Africa, Cape, Sneeubergen, Graaff Reinet, *Drège 2186* (K, lectotype; B, S, isolectotypes).

Plants usually small, 2.5–15(–20) cm high, unbranched and with the stem entirely subterranean. *Corm* to 1.5 cm in diameter; tunics of medium to coarse pale fibers. *Leaves* usually (–2)3–4(–6), erect and usually exceeding the inflorescence, or falcate, 0.5–3.5 cm wide, lightly pubescent, rarely glabrous, the margins always ciliate, often undulate to lightly crisped. Stem entirely subterranean, cormiferous at the nodes. *Spathe* enclosing the inflorescence solitary, herbaceous, often pubescent. *Flowers* several to many, fugaceous, white, blue, or yellow to pale brown, the nectar guide yellow, heavily scented; outer tepals broadly lanceolate, 2–3.5 cm long, the limb 1–2.5 cm long; inner tepals 1.6–3.0 cm long, linear-spathulate to narrowly lanceolate and ± erect or outspread. *Filaments* (3–)5–10 mm long, usually united only at the base; *anthers* 3–5 mm long. *Style branches* 7–15 mm long, the crest 8–15 cm, ± linear to lanceolate. *Capsule* enclosed by the spathe and leaf bases, soft walled; *seeds* with ± spongy testa. Chromosome number $2n = 20, 40$.

Flowering time: July to September.

Distribution: Clay or sandy slopes and flats from Namaqualand in the north to the Grahamstown district in the east.—Fig. 17.

Moraea ciliata is extremely specialized vegetatively, being much reduced in size and lacking an aerial stem. Though seedlings have a fairly typical, long, channeled leaf, mature plants have short spathelike leaves, the inner one of which encloses the inflorescence. While vegetatively specialized and reduced, the flowers of species in section *Acaules* are little modified from the basic pattern in *Moraea*.

Moraea ciliata occurs in a variety of color forms, either blue, white, yellow, or brown and is very characteristically sweet scented. It has two close allies which are very alike vegetatively. *Moraea macronyx*, a high altitude species is always recognized by its very long tepal claw and relatively shorter limb, and by rather corklike corm tunics. *Moraea tricolor* has quite differently arranged tepals with a relatively short claw and outspread limb and very broad style crests. The general appearance of this flower is of parts closely held together in contrast with

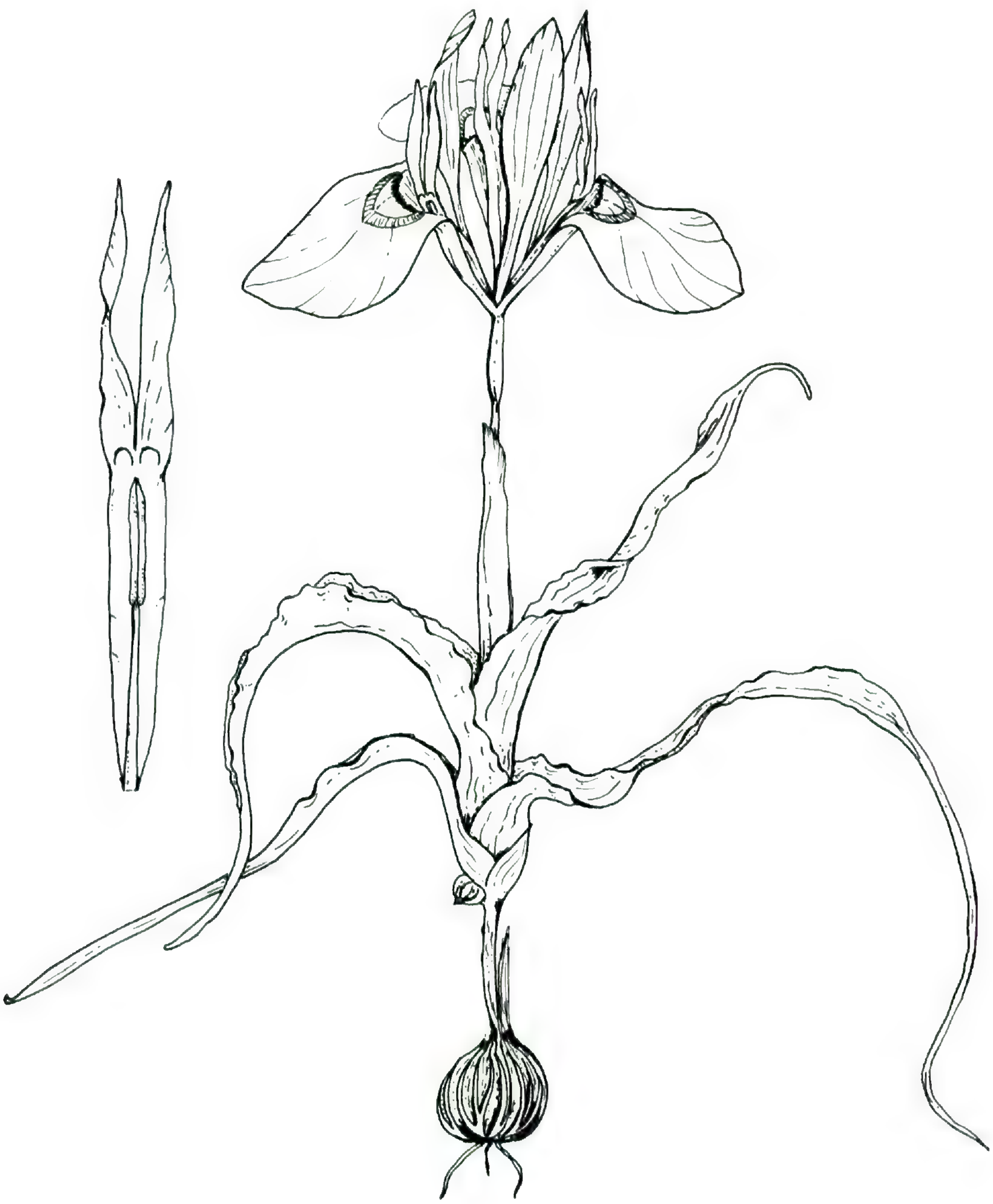


FIGURE 16. Morphology of *Moraea ciliata* (life size) with style branch and stigma enlarged.

the narrow, laxly arranged tepals and narrow style crests of *M. ciliata*. Most forms of *M. ciliata* are diploid, $2n = 20$, but a polyploid population has been found on clay soil in the Caledon district where *M. ciliata* was sympatric with *M. tricolor*. At this locality *M. tricolor* had $2n = 20$, in contrast to the more usual $2n = 18$.

Two species are treated as synonymous with *M. ciliata*: *M. macrochlamys*

is regarded as a robust form although from a region peripheral to the general range of the species, while *M. hantamensis* from the Calvinia district matches exactly plants from the Cape Peninsula, the type locality.

Moraea minuta, described at the same time as *M. ciliata* by the younger Linnaeus and often regarded as a synonym, is not included as accurate typification is not possible (see under excluded species).

Moraea ciliata is a particularly widespread species, ranging from Namaqualand in the north to near Grahamstown in the east, and occurring in all areas between, including isolated sites in the arid Great Karoo. Though it is tolerant of very varied conditions from high rainfall on the Cape Peninsula (ca. 762 mm) to less than 127 mm in parts of Namaqualand and the Karoo, it responds only to winter rainfall, and in the parts of the Karoo which now receive mainly summer rains, the existing populations are almost certainly relictual.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Top of Spektakel Pass, W of Springbok (DA), *Goldblatt 638* (BOL). Springbok (DB), *Salter 915* (BOL). Flats near Okiep, *Goldblatt 637* (BOL).

30.17 (Hondeklipbaai): 8 km SW of Kamieskroon (DB), *Acocks 19317* (K, NBG, PRE). 65 km S of Springbok on Leliefontein road, *Nordenstam 664* (NBG, S).

30.18 (Kamiesberg): Between Garies and Bitterfontein (C), *Leipoldt 3848* (BOL). Near Leliefontein, Kamiesberg (AC), *Goldblatt 633* (BOL).

31.18 (Van Rhynsdorp): Holrivier, Vredendal (CB), *Booysen 152* (NBG). Heerenlogement mountains (DC), *Fisher 9* (NBG). Olifants River barrage (DD), *Compton 11168* (NBG).

31.19 (Calvinia): Blaauwkrans, 50 km NW of Calvinia (AB), *Lewis 2754* (SAM). Near Nieuwoudtville (AC), *Barker 6523* (NBG); *Lewis 5846* (NBG); *Leipoldt 3849* (BOL). Glenlyon, Nieuwoudtville, *Lewis 5885* (NBG); *Strauss s.n.* (NBG-90218). 16 km E of Nieuwoudtville (AD), *Lewis 5865* (NBG). Calvinia commonage (BD), *Marloth 10237* (PRE). Hantam Mountain, *Meyer 13* (B); *Marloth 12802* (PRE).

31.20 (Williston): 4 km NW of Middelpos (CC), *Acocks 18460* (K, PRE).

31.24 (Hanover): Verlate Plaats (AC), *H. Bolus 8746* (BOL). Compasberg, Sneeubergen (D), *Drège 2186* (K, S).

32.18 (Clanwilliam): Near Redelingshuys (AD), *Loubser 2171* (BOL). Boschkloof (BB), *Schlechter 8472* (BOL, K, PRE, S).

32.19 (Wuppertal): Pakhuis Pass (AA), *Salter 2449* (BOL); *Compton 6616* (NBG). Welbedacht Kloof, Cedarberg, *Stokoe s.n.* (SAM-55670).

32.20 (Sutherland): Top of Verlate Kloof (DA), *Marloth 9647* (PRE); *Goldblatt 548* (BOL). Voelfontein (B), *Hall 196, 197* (both NBG).

33.18 (Cape Town): Donkergat (AA), *Goldblatt 427* (BOL). Between Moorreesburg and Piketberg (BB), *Barker s.n.* (BOL-20211). Signal Hill, Cape Town (CD), *Thunberg s.n.* (UPS); *Marloth 166* (BOL, PRE); *Barnard s.n.* (BOL, SAM); *Zeyher 30* (PRE, SAM). Near Durbanville (DC), *Salter 2672* (BOL).

33.19 (Worcester): Hills near Porterville (AA), *Schlechter 10718* (BOL, BR, K, PRE, S). Saron, *Schlechter 7863* (K, PRE, S). Cold Bokkeveld (AB), *Schlechter 8890* (BOL, BR, PRE, S). Gydo Pass, *Leipoldt s.n.* (BOL). Swaarmoed, Ceres district (AD), *Loubser 983* (NBG). Top of Hex River Pass (BD), *Stayner s.n.* (NBG-88046). Worcester (CB), *Steyn 202* (NBG).

33.20 (Montagu): Matjesfontein, near station (BA), *Goldblatt 658* (BOL). Whitehill Ridge, *Compton 3261* (BOL, NBG). Montagu (CC), *Page s.n.* (BOL-17719).

33.22 (Oudtshoorn): Meiringspoort (BC), *Loubser 995* (NBG).

33.26 (Grahamstown): Carlisle bridge (AA), *Bayliss 2306* (MO).

34.18 (Simonstown): Kommetje, Cape Peninsula (AB), *Wolley Dod 1657* (BOL). Vlei at Chapmans Bay, *Wolley Dod 1651* (BOL).

34.19 (Caledon): Between Eseljacht and Queen Anne (AA), *Goldblatt 2498* (MO).

34.20 (Bredasdorp): Wydgelegen (AD), *Barker 4543* (NBG).

34.21 (Riversdale): Oakdale (A), *Muir 2690* (BOL).

13. **Moraea macronyx** Lewis, Ann. S. African Mus. 40: 115. 1954. TYPE: South Africa, Cape, Gydo Pass, *Lewis s.n.* (SAM-61920).

Plants similar in habit to *Moraea ciliata*, 9–18(–25) cm high. *Corm* to 1.3 cm in diameter; tunics pale, of fibers or entire corklike layers, cormiferous at the base and bearing suckers. *Leaves* 3, falcate, glabrous or lightly pubescent, the margins straight to undulate, ciliate. *Spathe* enclosing the inflorescence solitary, glabrous to pubescent. *Flowers* several, pale yellow and white; outer tepals 4–6 cm long, the claw 2.5–4 cm long, up to about twice the length of the limb, ca. 2 cm wide; inner tepals 3–4.5 cm long, linear-lanceolate, obtuse, to 7 mm at the widest point. *Filaments* 1.2–1.8 cm long, joined for ca. 6 mm; *anthers* linear, to 9 mm long, apiculate. *Style branches* ca. 2 cm long, to 5 mm wide, the crests to 2.5 cm long. *Capsule* and *seed* not known. Chromosome number $2n = 20$.

Flowering time: September to mid October.

Distribution: Southern Cold Bokkeveld and east to the Laingsburg district and the Long Kloof.—FIG. 17.

Moraea macronyx, described only quite recently, is closely allied to the well-known and widespread *M. ciliata*, and falls entirely within the geographic range of this species. It differs consistently from *M. ciliata* and remains quite distinct from forms of *M. ciliata* growing in the same area, which indicates that specific status is well deserved. It can readily be distinguished from other species of section *Acaules* by the very long claw to the tepals, which are at least twice as long as the limb. The corm tunics are also distinctive, being entire and peculiarly soft, as if composed of loosely packed cells; *M. ciliata* has, in contrast, fibrous tunics, though occasionally these approach the type found in *M. macronyx*.

Though originally believed to occur only in the Cold Bokkeveld, *M. macronyx* has recently been recorded from the Hex River-Matroosberg area, Tweedside, and well to the east, in the Long Kloof near Avontuur. All records have in common a fairly high altitude, though plants apparently grow in both sandy and clay soils, this also being a feature of *M. ciliata*. The distribution indicates an unusually wide disjunction for the genus, and *M. macronyx* may well be discovered in intervening areas in suitable habitats.

SOUTH AFRICA. CAPE: 32.19 (Wuppertal): Leeurivier, Cold Bokkeveld (CD), *Barker 3802* (NBG); *Lewis 1397* (SAM); *Mauve 4679* (K, PRE, STE). Helpmekaar, Cold Bokkeveld, *Hanekom 1291* (PRE). De Keur, *Barker 3118* (NBG); *Loubser 2020* (NBG).

33.19 (Worcester): 9 km N of top of Gydo Pass (AB), *Lewis 2533* (SAM); *Johnson 504* (NBG, STE). Elandsfontein, *Martin s.n.* (BOL). Groenfontein, *Barker 3113* (NBG). Welvaart, foot of Sandrift Peaks (BC), *Oliver 5071* (STE, MO). Near Matroosberg station (BD), *Mauve & Oliver 1265* (MO, STE).

33.20 (Montagu): Tweedside (AB), *Barker 7468* (NBG).

33.23 (Willowmore): Avontuur (CA), *Goldblatt 2860* (K, MO, NBG, PRE).

14. **Moraea tricolor** Andrews, Bot. Rep., *tab.* 83. 1800. TYPE: Illustration in Bot. Rep., *tab.* 83.

M. ciliata (L.f.) Ker var. *tricolor* (Andrews) Baker, Fl. Cap. 6: 11. 1896.

Iris fugax Persoon, Syn. Pl. 1: 54. 1810, nom. illeg., superfl. pro *Moraea tricolor* Andrews. TYPE: As for *M. tricolor* Andrews.

M. barbigera Salisb., Trans. Hort. Soc. London 1: 306. 1812. TYPE: Illustration in Bot. Mag., *tab. 1012* (*M. ciliata* var.).

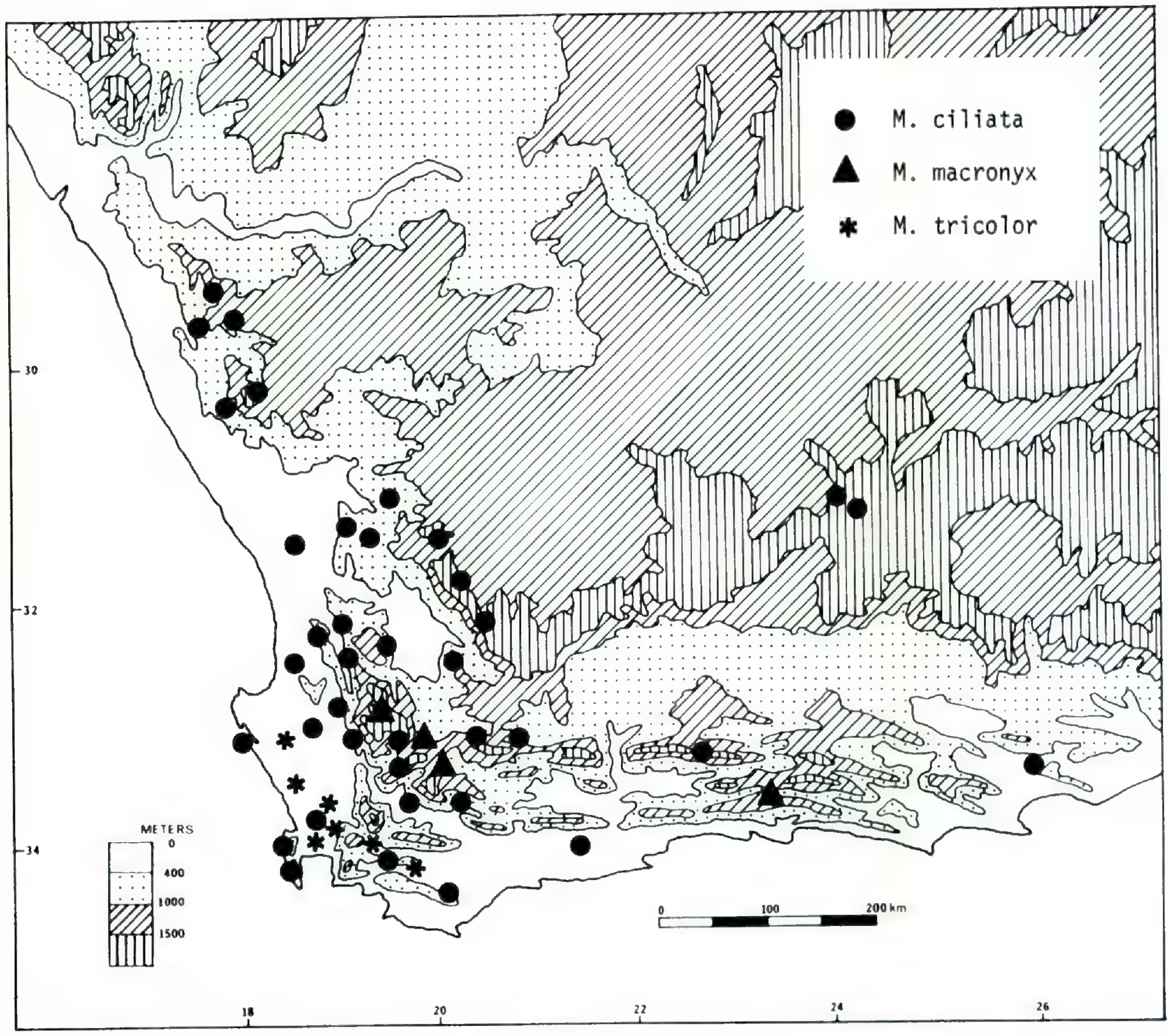


FIGURE 17. Distribution of *Moraea ciliata*, *M. macronyx*, and *M. tricolor*.

M. ciliata var. *barbigera* (Salisb.) Baker, Fl. Cap. 6: 11. 1896.
M. duthieana L. Bol., Ann. Bolus Herb. 4: 113. 1927. TYPE: South Africa, Cape, 15 km W of Stellenbosch, *L. Bolus s.n.* (BOL-18529, holotype; K, isotype).

Plants small, 5–15 cm high, unbranched, the stem entirely subterranean. *Corm* ca. 1.5 cm in diameter; tunics of medium to coarse, pale fibers. *Leaves* usually 3, ± erect, exceeding the spathe, glabrous or lightly pubescent, the margins ciliate, usually straight, or lightly undulate. *Stem* subterranean, cormiferous at the nodes. *Spathe* enclosing the inflorescence, solitary, glabrous or lightly pubescent. *Flowers* several, fugaceous, yellow, red or light purple, the nectar guide yellow; outer tepals 2–2.5 cm long, lanceolate, outspread, the limb 8–13 mm long; inner tepals 2–2.5 cm long, lanceolate, distinctly clawed, spreading. *Filaments* 3–4 mm long, united at the base only; *anthers* 2.5–3 mm long. *Style branches* to 5 mm long, the crests 8–10 mm long, exceeding the style branches and broadly triangular, ca. 5 mm wide. *Capsule* enclosed in the inflorescence spathe and leaf bases, soft walled; *seeds* unknown. Chromosome number $2n = 18, 20$.

Flowering time: Late July to mid September.

Distribution: Moist clay slopes or wet depressions in the Caledon, Cape, and Malmesbury districts.—FIG. 17.

Moraea tricolor was first regarded as a species distinct from its close relative *M. ciliata*, by Andrews in 1800, and subsequently by Salisbury (in 1812) and Louisa Bolus (in 1927); the latter two persons gave the plant different names primarily because of color differences. The type of *M. tricolor*, an illustration, is clearly the beautiful red-flowered form from the Darling district of the south-western Cape. A yellow form, also found in this area, is more common, extending north and east to Hopefield and Stellenbosch. Both red- and yellow-flowered forms from this western coastal belt are glabrous, with only the leaf margins bearing minute ciliate hairs. To the east, in the Caledon district, a third form with a pink to purple flower is, by contrast, markedly pubescent.

Cytologically *M. tricolor* is variable, the western forms (two populations examined) have a diploid number of $2n = 18$; the Caledon forms (again two sites studied) have $2n = 20$. This latter number is basic in subgenus *Moraea*, and occurs in all other species of section *Acaules*. This suggests *M. tricolor* is specialized, and plants with $2n = 18$ represent aneuploid derivatives from the ancestral group. The occurrence of both $2n = 20$ and 18 in this species is noteworthy as heteroploidy is very unusual in the genus. Flowers of the $2n = 20$ and $2n = 18$ forms are, however, so similar that it is not possible to separate the forms taxonomically.

Moraea tricolor, probably recently evolved from the widely distributed *M. ciliata*, presumably maintains its identity by virtue of the cytological differences between it and *M. ciliata*: the pink Caledon forms with $n = 10$ are isolated from sympatric populations of *M. ciliata* by polyploidy in the latter; while the west-coast forms with $n = 9$ are isolated by aneuploid differences.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Near Hopefield (AB), *Axelson 206* (NBG). Near Darling (AD), *Lewis Grant 4610* (MO). Klipheuwel, damp flats (DA), *Lewis 5601* (NBG). 25 km S of Malmesbury, *Goldblatt 2178* (MO). Damp places 15 km W of Stellenbosch (DD), *L. Bolus s.n.* (BOL-18529). Upper flats, Stellenbosch, *Duthie 505* (BOL); *Garside 266* (K).

34.18 (Simonstown): Between Strand and Gordons Bay (BB), *Parker 4331* (K).

34.19 (Caledon): Drayton siding E of Caledon (BA), *Goldblatt 2516* (M). 18 km E of Caledon, *Barker 10615* (NBG). Fairfield (BD), *Lewis 5285* (NBG).

Section 3. **Deserticola** Goldbl., Ann. Missouri Bot. Gard. 63: 7. 1976. TYPE: *Moraea bolusii* Baker.

Plants small to medium, few to several branched. *Corms* with outer layers of tunics dark brown to black, the fibers fairly coarse. *Leaf* solitary, basal, canaliculate or terete. *Stems* well developed, usually branched, often frequently. *Flowers* with unguiculate, reflexed tepals with the inner whorl entire and large. *Capsules* clavate and exserted; *seeds* small and angled in those species in which fruits are known. Basic chromosome number $x = 10$.

Distribution: Dry areas of the north western Cape and extreme southern South West Africa.

The section comprises four closely related species, all occurring in very arid areas in southern Africa. The affinities of section *Deserticola* lie with species such as *Moraea serpentina* of section *Moraea*, which has a similar asymmetric corm with dark tunics. The difference between the sections is in leaf number, with *M. serpentina* and other species of section *Moraea* having two or more, often several, leaves. Cytologically, section *Deserticola*, with $n = 10$ and a characteristic karyotype of five long acrocentric chromosome pairs and five much shorter ones, is close to section *Moraea*, especially *M. serpentina* and *M. tortilis* where the same pattern is found.

15. **Moraea saxicola** Goldbl., sp. nov. TYPE: South Africa, Cape, 5 km W of Steinkopf, *Goldblatt 3057* (MO, holotype; K, NBG, PRE, S, isotypes).—FIG. 18.

Planta (10–)20–40 cm alta, caule ramoso. *Cormus* ca. 2 cm latus, tunicis atrobrunneis, supra productum. *Folium* solitarium, canaliculatum, marginibus hyalinis, crassis, undulatis ad crispis; folium raro teres. *Flores* pallidi coerulei aut albi ad cremei; *tepala exteriora* 2.5–4 cm longa, unguis 1–1.5 cm longa; *tepala interiora* breviora, reflexa. *Capsula* et *semina* ignota.

Plants (10–)20–40 cm high, usually several branched. *Corms* ca. 2 cm in diameter; tunics dark brown, finely netted, extending upward in a neck. *Leaf* solitary, somewhat exceeding the inflorescence, usually canaliculate, 4–8 mm wide, with thickened yellow margins, either straight or undulate, sometimes crisped; juvenile plants often with terete leaves coiled near the apex. *Stem* erect, with short branches held close to the axis. *Spathes* usually dry at flowering time, often lacerated; inner spathe 3–6 cm long, the outer about 1 cm shorter. *Flowers* pale blue or white to cream, the nectar guides yellow to orange; *outer tepals* 2.5–4 cm long, the limb ca. 1.5–2 cm, reflexed at ca. 45°; inner tepals smaller and shorter, also reflexed. *Filaments* 7–13 mm long, joined in the lower half; *anthers* 6–9 mm long, slightly exceeding the stigma, the pollen white. *Style branches* 8–15 mm long, the crests 1.0–1.5 cm long, lanceolate. *Capsules* not known. Chromosome number $2n = 20$ (*Goldblatt 3057*, type collection).

Flowering time: September to October.

Distribution: Stony slopes and flats on clay soils in Namaqualand, also occasionally on granite.—FIG. 18.

Although until recently very poorly collected, *Moraea saxicola* is fairly common throughout Namaqualand, and it is particularly abundant wherever clay and shale outcrops occur. It blooms rather late in the season, mainly in October, which perhaps accounts for the paucity of collections, since this is generally after the flowering season in Namaqualand. Flowers open after 1 P.M. and in the north after 3 P.M., which is another reason it has been overlooked.

In northern Namaqualand, on the clay soils near Steinkopf and at Spektakel Pass, a pale blue form occurs, while to the south, from near Garies to Nuwerus, plants have creamy white flowers. Leaves are generally broad and slightly undulate but crisped margins may be found in plants in the south. Unusually for *Moraea*, young plants have a juvenile leaf form which is terete and coiled only near the apex. By the time these plants reach flowering age, the leaf is usually typically channelled, but occasionally, as for example a collection from

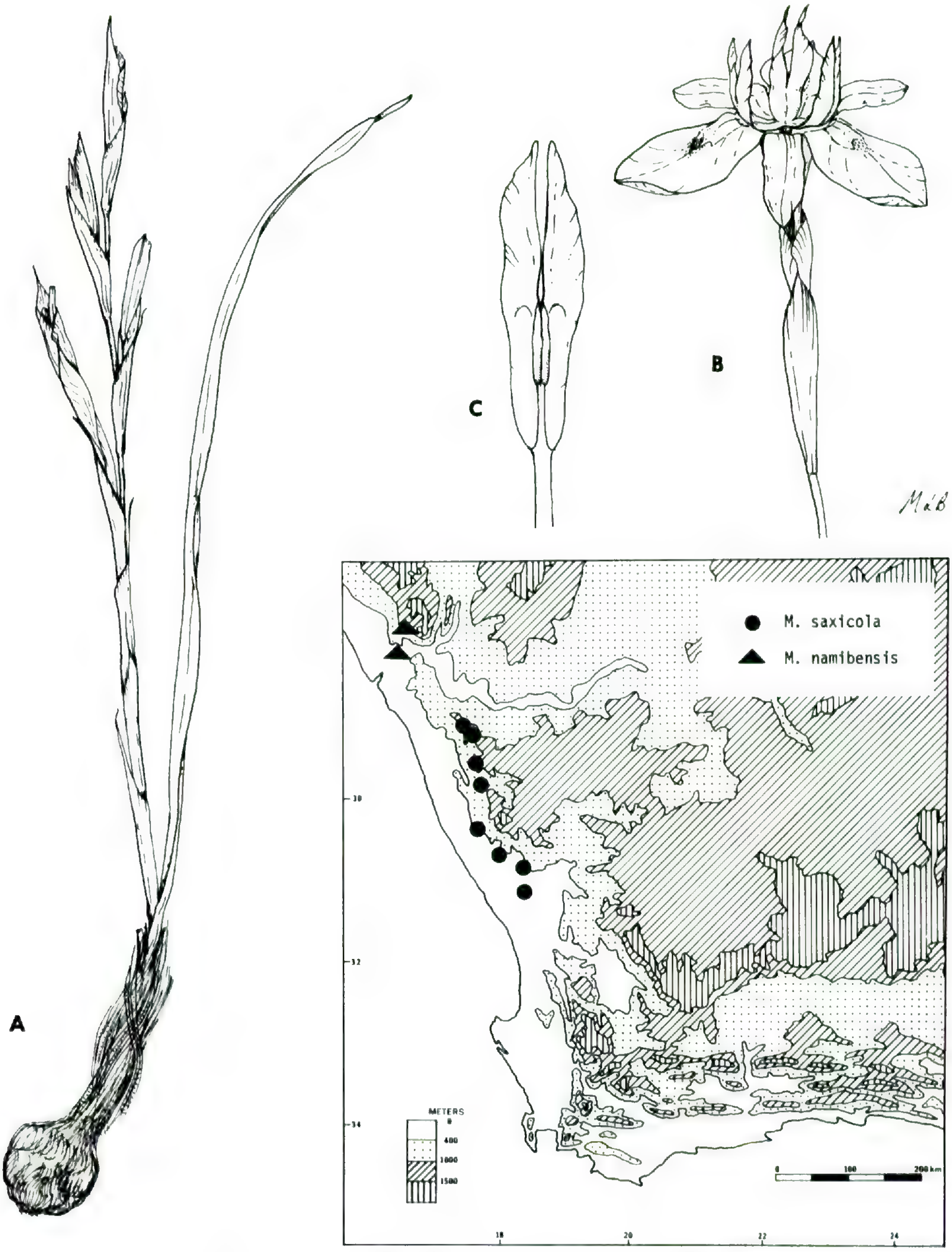


FIGURE 18. Distribution of *Moraea saxicola* and *M. namibensis* with morphology of *M. saxicola*.—A. Habit (×0.5).—B. Flower (life size).—C. Style branch and stamen (enlarged).

south of Springbok, *Acocks 19584*, plants with a juvenile leaf produce flowers. In the case of this collection it is not known whether plants of this population have this terete leaf throughout their lives.

Moraea saxicola is allied to *M. bolusii*, a common yellow-flowered Namaqua-

land species with an undulate leaf, and to the newly described *M. macgregorii*, which grows to the south in the Calvinia-Van Rhynsdorp area and also blooms in the late afternoon.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Ca. 4 km W of Steinkopf (BA), *Wisura 2488* (NBG); *Strauss 140* (NBG); *Goldblatt 3057* (K, MO, NBG, PRE, S). Koufontein (BC), *Herre s.n.* (STE-11834). Ca. 22 km W of Springbok (CA), *Rodin 2190* (BOL, K, MO). E slopes of Spektakelberg, *Goldblatt 3047* (MO, NBG, PRE, S). 45 km S of Springbok (DD), *Acocks 19584* (K, M, NBG, PRE).

30.17 (Hondeklipbaai): 10 km N of Garies (DB), *Goldblatt 4256* (MO).

30.18 (Kamiesberg): Between Garies and Bitterfontein (CC), *Goldblatt 4257* (MO).

31.18 (Van Rhynsdorp): Near Nuwerus (AB), *Goldblatt 4258* (MO, NBG). 30 km SW of Nuwerus (AC), *Acocks 19596* (K, M, NBG, PRE).

16. **Moraea macgregorii** Goldbl., sp. nov. TYPE: South Africa, Cape, foot of Van Rhyns Pass, *Goldblatt 3097* (MO, holotype; NBG, isotype).—FIG. 19A–B.

Planta 12–25 cm alta, caule ramoso. *Cormus* ca. 2 cm latus, tunicis brunneis, reticulatis supra extensis. *Folium* solitarium, canaliculatum, marginibus hyalinis. *Flores* pallidi coerulei-lilacini; tepala exteriora ca. 3 cm longa, limbis ca. 1.5 cm longis; tepala interiora ca. 2.5 cm longa, reflexa. *Capsula* ca. 1.5 cm longa, clavata, rostrata; *semina* angulata.

Plants medium to small, 12–25 cm high. *Corm* ca. 2 cm in diameter; tunics of light brown, fine-netted fibers extending upward in a neck. *Leaf* solitary, much exceeding the inflorescence, trailing, 3–4 mm wide, canaliculate, the margins thickened. *Stem* flexuose, several branched. *Spathes* herbaceous in the lower part to completely dry at flowering, occasionally lacerated; inner spathe 3–3.5 cm long, the outer slightly shorter. *Flowers* pale lilac, the nectar guides prominent, golden; outer tepals ca. 3 cm long, the limb ca. 1.5 cm long, reflexed to 45°; inner tepals also reflexed, narrowly lanceolate, ca. 2.5 cm long. *Filaments* 1.5 cm long, joined in the lower half; *anthers* 3–4 mm, the pollen whitish. *Style branches* ca. 1.8 cm long, the crests narrow, to 1 cm long. *Capsule* ca. 1.5 cm long, clavate, distinctly beaked to ca. 1.5 mm long; *seeds* small, angled. Chromosome number $2n = 20$ (*Goldblatt 3097*, type collection).

Flowering time: October.

Distribution: Dry stony, lower mountain slopes in the Van Rhynsdorp district; flowers opening about 4:00 P.M.—FIG. 20.

Collections of a strange *Moraea*, often identified as *M. fugax*, prompted the search for living populations of the species now described as *M. macgregorii*. The type collection was made at the foot of Van Rhyns Pass between Van Rhynsdorp and Nieuwoudtville, in an area frequently visited and passed by botanists. The reason for the paucity of earlier collections and lack of good flowering material was immediately evident: flowers of *M. macgregorii* only open after 4:00 P.M.—on cooler days after 4:30 P.M.—and fade in the early evening, thus lasting only about two and one-half hours. This is probably the shortest flowering period of any species of *Moraea*.

Vegetatively there is little to distinguish *M. macgregorii*; it has a solitary, rather narrow undulate leaf, a short, branched stem, and rather dry, scarious spathes. Apart from the single leaf, it resembles *M. serpentina*, with which it grows. The flower is, however, striking, and the pale bluish tepals with their

FIGURE 19. *Moraea* species.—A–B. *M. macgregorii*.—A. Whole plant (×0.75).—B. Style branch and stamen (×1.5).—C. *M. bolusii* (life size).

long very narrow claw, narrow reflexed limb, and characteristic nectar guides all indicate that *M. macgregorii* is a quite distinct species. Though apparently isolated in section *Deserticola*, it is most nearly allied to *M. saxicola* and *M. bolusii*, both characteristic species of the arid regions of Namaqualand and the Van Rhynsdorp area.

The species is named in honor of the MacGregor family, farmers in the Nieuwoudtville district who have for many years been prominent in the area as nature lovers and avid conservationists. Few can equal their knowledge of the unique and striking flora of the Nieuwoudtville district and their help, unstint-

ingly extended to all visitors to the area, botanists and tourists alike, is acknowledged here with gratitude.

SOUTH AFRICA. CAPE: 31.19 (Calvinia): Foot of Van Rhyns Pass near Nieuwoudtville (AC), *Barker 9653* (NBG, S, STE); *Goldblatt 3072* (MO, NBG), *3097* (K, MO, NBG, PRE).

17. **Moraea namibensis** Goldbl., sp. nov. TYPE: South West Africa, sandy flats near Udabib, *Merxmüller & Giess 3299* (W, holotype; M, PRE, isotypes).

M. edulis (L.f.) Ker, sensu Sölch, Prodr. Fl. S.W. Afr. 155: 11. 1969.

Planta 12–40 cm alta, pauciramosa. *Tunici* cormi tenui-reticulati. *Folium* solitarium, basale, canaliculatum. *Flores* albi ad caerulei; tepala exteriora 3.5–4 cm longa, lanceolata, limbus ca. 2 cm; tepala interiora ca. 3.5 cm longa, integra, lanceolata. *Filamenta* connata in pars dimidia. *Rami styli* ca. 1 cm longi, cristae ad 1.5 cm longa.

Plants erect, 12–40 cm high. *Corm* ca. 2 cm diameter; tunics dark, finely reticulate. *Leaf* solitary, inserted at ground level, linear, canaliculate, exceeding the inflorescence. *Stem* erect, usually several branched. *Spathes* several flowered, herbaceous with membranous, brown-tipped apices, 3.5–6 cm long; outer spathe about half the length of the inner. *Flowers* white or pale blue, the nectar guides yellow; outer tepals ca. 4 cm long, the limb 2 cm long, flexed at the knee; inner tepals ca. 3.5 cm long, lanceolate and obtuse, (apparently erect). *Filaments* ca. 1 cm long, joined for half their length; *anthers* 6 mm long. *Style branches* ca. 1 cm long, the crests lanceolate, 1.5 cm long. *Capsule* and *seeds* unknown.

Flowering time: August.

Distribution: Sandy flats, southwestern South West Africa.—FIG. 18.

This species, known only from two gatherings, is quite distinct from *Moraea fugax*, to which, as *M. edulis*, it was assigned in Merxmüller's *Prodromus einer Flora von Südwestafrika*. While the flowers of the two species are similar, the leaf, produced from the base of the stem in *M. namibensis*, contrasts with an insertion high on the stem, just below the spathes, in *M. fugax*. The corm tunics of *M. namibensis* are also distinctive, being dark brown and forming a fine reticulum in contrast to the pale, often rather coarse fibers of *M. fugax*. Although all too poorly known, *M. namibensis* appears to be most closely related to the group of Namaqualand species which embraces the undulate-leafed *M. bolusii* and *M. saxicola*, the distinctive species found mainly on clay outcrops in Namaqualand.

Moraea namibensis occurs in the extreme south of the Namib Desert in the southwest corner of South West Africa, an area which receives a small amount of winter precipitation. It is the only winter rainfall species of *Moraea* recorded outside the Cape Province.

SOUTH WEST AFRICA. 27.16 (Witpütz): Sandy flats near Udabib (CB), *Merxmüller & Giess 3299* (M, PRE, WIND). Zebrafontein, Witpütz-Sud (D), *Merxmüller & Giess 28752* (M).

18. **Moraea bolusii** Baker, Handbook Irid. 57. 1892. TYPE: South Africa, Cape, near Okiep, *H. Bolus 6574* (K, lectotype; BOL, isolectotype).—FIG. 19C.

Plants 7–20 cm high, few branched, solitary or in clumps. *Corm* 1–2 cm in diameter; tunics of coarse black fibers usually extending upwards in a neck.

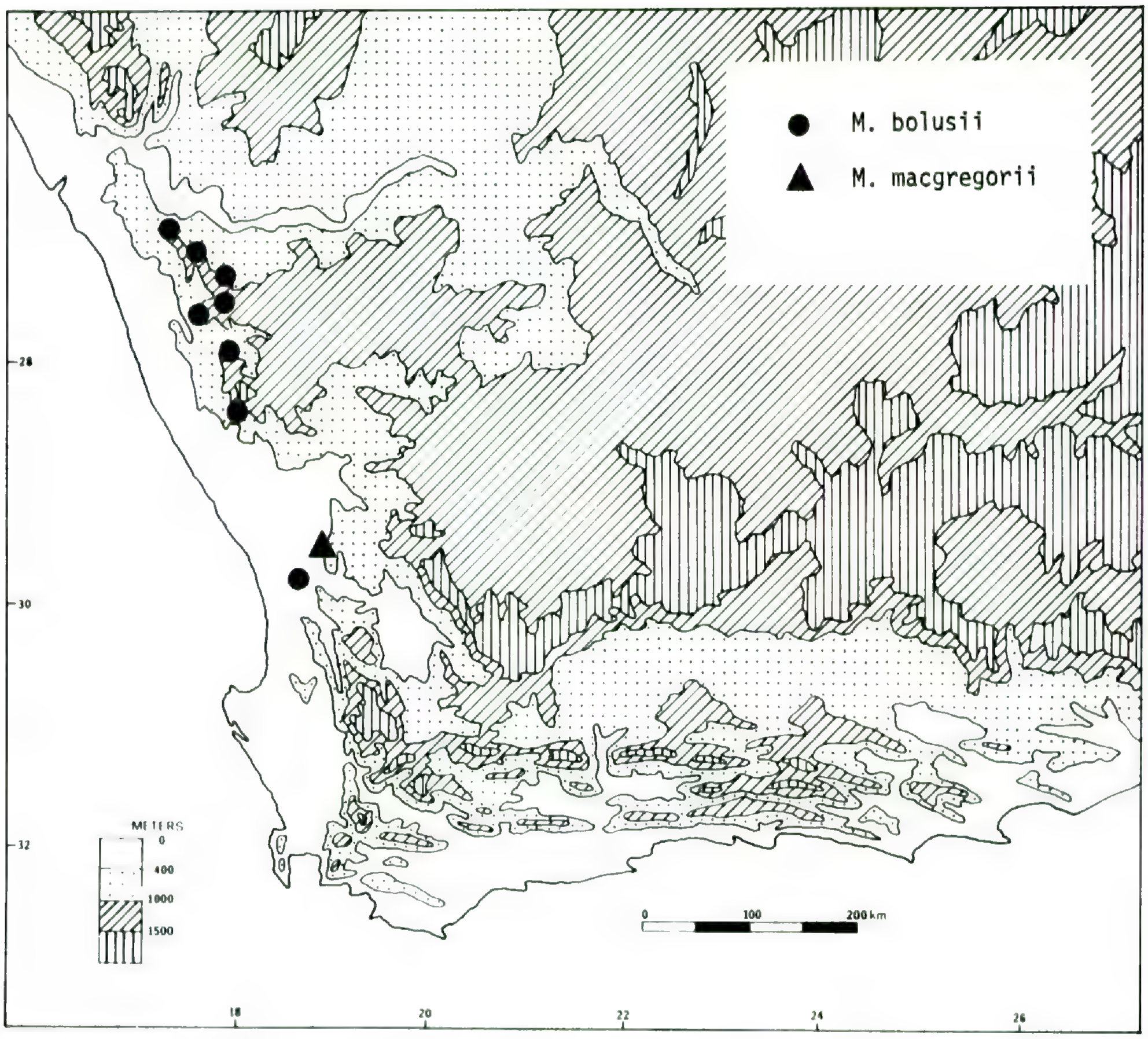


Figure 20. Distribution of *Moraea bolusii* and *M. macgregorii*.

Leaf solitary, glabrous, often longer than the stem, erect or trailing, linear, canaliculate, the margins usually undulate. *Stem* simple or few branched, the branches held close to the axis, the cauline bracts dry and membranous. *Spathes* usually dry at flowering time, acute or lacerated; inner spathe 3–4.5 cm long, the outer ± half the inner. *Flowers* usually pale yellow and white, occasionally pale lilac; outer tepals 2.6–3.3 cm long, broadly lanceolate, to 1.3 cm wide, reflexed to 45°; inner tepals ca. 2.5 cm long, reflexed. *Filaments* 7–10 mm long, joined for about two-thirds of their length; *anthers* ca. 6 mm long. *Style branches* ca. 1 cm long, the crests 1–1.5 cm long, broadly ensiform. *Capsule* and *seeds* not known. Chromosome number $2n = 20$.

Flowering time: September to October.

Distribution: In shallow sandy soils from the Van Rhynsdorp district north to Namaqualand where it is comparatively common.—Fig. 20.

Moraea bolusii, a fairly widespread Namaqualand species, was first collected by Bolus and by Schlecter in the late nineteenth century and was described by Baker. Subsequent collections have been few, but personal observation has

shown it to be relatively common, especially in the Springbok district growing in shallow sandy soil, on flats or slopes.

The species can usually be recognized even when not in flower as its fairly wide, solitary, undulate leaf is distinctive. The flower is much like that in most species of section *Deserticola*, with quite broad, reflexed inner tepals. The flower, however, is typically yellow with paler style branches and crests, while most representatives of the section are blue flowered, particularly its closer allies *M. saxicola* and *M. macgregorii*. A collection from near Klawer (*Compton s.n.*) which has a pale lilac flower is also referred to *M. bolusii* somewhat expanding the concept and range of this species. The Klawer specimens have the typical undulate leaf, black corm tunics, and few-branched scape and thus differ mainly in flower color.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Kinderle, Steinkopf (BC), *Hall 843* (NBG). Foot of quartzite hill, between Okiep and Steinkopf, *Goldblatt 2772* (MO). Near Okiep (DB), *H. Bolus 6574* (K, BOL). Roadside N of Okiep, *Goldblatt 632* (BOL). Hills E of Nababeep, *Goldblatt 631* (BOL); *Strauss 141* (NBG). Leospoort near Concordia, *Schlechter 11357* (BOL, BR, K). 50 km SW of Springbok, granite hills (DC), *Acocks 19584* (NBG, PRE).

30.18 (Kamiesberg): 9 km S of Garies (CA), *Lewis 2328* (SAM).

31.18 (Van Rhynsdorp): Near Klawer (DC), *Compton s.n.* (BOL, NBG-58800).

Without precise locality: Richtersveld, *Meyer 48* (STE).

Section 4. **Subracemosae** Baker [as subgenus *Eumoraea* (section) *Subracemosae*], Fl. Cap. 6: 10. 1896, pro parte, emend. Goldbl., Ann. Missouri Bot. Gard. 63: 7. 1976. TYPE: *Moraea fugax* (de la Roche) Jacq.

Plants small to large, few to many branched. *Corm* tunics pale, of medium to fine fibers. *Leaves* 1 or 2, inserted well above ground level at the base of the first branch. *Stem* branching freely, or with a few clustered branches. *Flowers* with entire, reflexed, unguiculate inner tepals. *Capsules* clavate-cylindrical, strongly beaked, often partly enclosed; *seeds* small, angular. Basic chromosome number, $x = 10, 8, 6$.

Distribution: Southwestern Cape and Namaqualand.

Section *Subracemosae*, as treated here, comprises only two species, the striking, many-branched *Moraea gracilenta* with $x = 10$, and the very variable aggregate species *M. fugax*, in which haploid numbers of $n = 8$ and $n = 6$ have been recorded. This range of chromosome numbers makes section *Subracemosae* appear as a bridge between the subgenera with $x = 10$ and $x = 6$, linking particularly subgenus *Moraea* to subgenus *Vieusseuxia*. The distinctive morphology of section *Subracemosae* with the peculiar leaf insertion and characteristic beaked ovary make it unlikely that this is the case. Derivation of the reduced chromosome number is accordingly suggested to have occurred independently in the two groups.

The similarity of karyotype in *M. gracilenta*, probably ancestral to the *M. fugax* complex, to the other sections of subgenus *Moraea* has been a major reason for including section *Subracemosae* here. The similarity is particularly close in section *Deserticola* and *M. serpentina* and *M. tortilis* of section *Moraea* where five large and five small chromosome pairs are found.

19. **Moraea gracilenta** Goldbl., sp. nov. TYPE: South Africa, Cape, sandy flats S of Pikenierskloof Pass, Piketberg district, *Goldblatt 3279* (MO, holotype; K, NBG, PRE, S, isotypes).—FIG. 21B–D.

M. edulis L.f. var. *gracilis* Baker, Handbook Irid. 56. 1892; Fl. Cap. 6: 21. 1896. TYPE: South Africa, Cape, Tulbagh Kloof to Pikeniers Kloof, *Zeyher 1647* (K, lectotype; PRE, S, isolectotypes).

Planta 30–80 cm alta, multiramosa. *Cormus* 1.5–2 cm diametro. *Folium* solitarium, lineare, canaliculatum. *Spathae* herbaceae, supra bruneae, apice acuta. *Flos* pallidus caeruleus-malvinus; tepala effusa; tepala exteriora 2–3 cm longa; interiora 1.8–2.8 cm. *Capsula* ca. 1 cm longa, rostrata.

Plants 30–80 cm high, many branched. *Corm* 1.5–2 cm in diameter; tunics of fine to medium pale fibers. *Leaf* solitary, canaliculate, linear, exceeding the inflorescence but usually trailing, inserted well above the ground at the base of the first branch. *Stem* erect and multibranched. *Spathes* herbaceous, becoming dry, the apices brown, acute; inner spathe 2.5–3.5(–4) cm long, the outer less than half the inner. *Flower* pale blue-mauve, strongly scented; outer tepals 2–3 cm long, ca. 8 mm at the widest point, lanceolate; inner tepals 1.8–2.8 cm long, 5–6 mm wide, spreading. *Filaments* ca. 5 mm long, united in the lower half; *anthers* 4–6 mm long, white. *Style* branches 7–9 mm long, the crests linear-lanceolate, 7–12 mm long. *Capsule* ca. 1 cm long, distinctly beaked; *seeds* angled. Chromosome number $2n = 20$.

Flowering time: Late September to November, extending to December at higher altitudes.

Distribution: Western coastal belt from Tulbagh Kloof to Clanwilliam, in sandy situations.—FIG. 21.

Moraea gracilenta has been known for many years, at least since the 1820s when Ecklon and Zeyher collected it near Tulbagh Kloof. Of the many systematists who studied Ecklon and Zeyher collections only J. G. Baker thought it worthy of taxonomic recognition and described it as *Moraea edulis* var. *gracilis*. It is indeed allied to *M. fugax*, the correct name for *M. edulis*, but it has several characteristics which indicate that it is a distinct species.

Firstly, it differs consistently from all the forms of the very variable *M. fugax* in its multibranched habit, very small blue flowers, and short inflorescence spathes and capsules. Secondly, it grows entirely within the geographic range of *M. fugax*, and the two occur within short distances of one another, yet their characteristics remain quite constant. Thirdly, the timing of flowering is markedly different: blooming occurs in the same months and the flowers of both species last a day only; however, while *M. gracilenta* blooms from about 3:30 P.M. to 7 P.M., flowers of *M. fugax* open between 11 A.M. and 12 noon and wilt by 6 P.M. The difference in flowering periods has been observed on three separate occasions in wild populations and appears to vary little. It is this differential that finally confirmed that *M. gracilenta* should be regarded as distinct from *M. fugax* and not simply a form of this widespread and variable species.

Moraea gracilenta occurs in the southwestern Cape along the western coastal

belt between Tulbagh and Clanwilliam in valleys and on flats. It prefers very sandy situations where its corm becomes buried 15–25 cm below the ground.

The chromosome number $n = 10$ suggests that *M. gracilenta* is primitive in section *Subracemosae*, and ancestral to *M. fugax*, which has recorded numbers of $n = 8$ and 6. Its multibranched habit seems consistent with this contention, though in leaf number, *M. fugax* appears more primitive since individuals of this species sometimes have two leaves. The chromosome number and karyotype of *M. gracilenta* clearly link this species, and thus section *Subracemosae*, to section *Moraea* and section *Deserticola* where similar karyotypes are found.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Riverbank near Clanwilliam (BB), *Goldblatt 3076* (MO); *Galpin 11482* (B, K, PRE). Eendekuil (DB), *Loubser 851* (NBG). Sandy areas between Eendekuil and Pikenierskloof Pass, *Goldblatt 3279* (K, MO, NBG, PRE, S), *3029* (MO, NBG, PRE).

32.19 (Wuppertal): Near Warm Baths, Olifants River valley (CA), *L. Bolus s.n.* (BOL-20323, K, PRE). Elandskloof, *Compton 16748* (NBG).

33.19 (Worcester): Tulbagh Kloof to Pikenierskloof (AC), *Zeyher 1647* (K, PRE, S). Tulbagh Kloof, *Compton 12399* (NBG); *Ecklon & Zeyher 23* (MO). Gydo (AD), *Leipoldt 3004* (BOL, K, PRE).

20. **Moraea fugax** (de la Roche) Jacq., Hort. Bot. Vindob. 3:14, *tab. 20.* 1776.—FIG. 21A.

Vieusseuxia fugax de la Roche, Descr. Pl. Nov. 33. 1776. TYPE: Illustration in van Hazen, Cat. Pl. 67. 1759 (lectotype).

Iris edulis L.f., Suppl. Pl. 93. 1781. TYPE: South Africa, Cape, exact locality uncertain, *Thunberg s.n.* (Herb. Thunb. 1123, UPS, lectotype).

Moraea edulis (L.f.) Ker, Bot. Mag. *tab. 613.* 1803; Baker, Fl. Cap. 6: 20. 1896.

Vieusseuxia edulis (L.f.) Link, Enum. Pl. Hort. Berol. 1: 56. 1821.

Moraea corniculata Lam., Tabl. Encycl. Méth. 1: 114. 1791; Encycl. Méth. 4: 227. 1797. TYPE: South Africa, Cape, *Sonnerat s.n.* (P, lectotype).

Iris longifolia Schneevoogt, Ic. Pl. Rar. *tab. 20.* 1792; Andrews, Bot. Rep., *tab. 45.* 1799. TYPE: Illustrations in Schneevoogt, Ic., Pl. Rar. *tab. 20* (lectotype).

Moraea longifolia (Schneevoogt) Sweet, Hort. Brit., ed. 2, 496. 1830, nom. illeg., non *M. longifolia* (Jacq.) Pers., 1805.

M. odora Salisb., Parad. Lond. Tab. 1: 10. 1805. TYPE: Illustration in Parad. Lond. 1: *tab. 10* (lectotype).

M. filicaulis Baker, Handbook Irid. 56. 1892. TYPE: South Africa, Cape, *Drège 2605* (K, lectotype).

M. diphylla Baker, Bull. Misc. Inform. 1906: 42. 1906. TYPE: South Africa, Cape, Olifants R., *Penther 734* (K, lectotype).

Plants medium to large, 12–40(–50) cm high, branched. *Corm* (1–)1.5–3 cm in diameter; tunics usually pale, rarely dark, of fine to medium fibers. *Leaf* usually solitary, occasionally 2, equal or unequal in length, subopposite, inserted well above ground immediately below the first branch, canaliculate, usually much exceeding the stem and trailing. *Stem* erect or more often somewhat falcate, with a conspicuous, long lower internode, the branches crowded, often semicorymbose. *Spathes* herbaceous, becoming dry, the upper margin light brown, apices attenuate; inner spathe 4–8 cm long, the outer ca. ⅓ the length of the inner. *Flowers* white, blue, or yellow, strongly scented; outer tepals 2.3–4.0 cm long, lanceolate, the limb ± equal the claw; inner tepals 2–3.5 cm long, erect or slightly reflexed, 5–8 mm wide. *Filaments* 6–10 mm long, joined in the lower half; *anthers* 4–8 mm long. *Style branches* 1.5–2 cm long, the crests lanceolate

FIGURE 21. Morphology and distribution of *Moraea fugax* and *M. gracilenta*.—A. *M. fugax* (life size).—B–D. *M. gracilenta*.—B. Habit ($\times 0.5$).—C. Flower (life size).—D. Style branch and stamen ($\times 1.5$).

6–16 mm long. *Capsule* clavate to cylindrical, distinctly beaked, 1.5–2.5 cm long; *seeds* many, angled. Chromosome number $2n = 16, 12$.

Flowering time: August to November, extending into December at higher elevations.

Distribution: Southern Cape to Namaqualand, frequently in sandy situations.—Fig. 21.

As circumscribed here, *Moraea fugax* is a large aggregate species consisting of numerous forms, including *M. filicaulis* (*M. diphylla*), none of which are given taxonomic recognition. No clear pattern of variation is evident as yet, but a very detailed analysis of the range of forms will undoubtedly prove rewarding. The occurrence of diploid numbers of $2n = 16$ and 12 is noteworthy, the heteroploidy in this species being all the more significant as $n = 8$ represents one of the few records intermediate between the common base numbers, $n = 10$ and $n = 6$, in *Moraea*. A combined cytological and morphological study should be all the more interesting in view of this.

The characteristic features of *M. fugax* are the leaf insertion, well above the ground and just below the first branch, and the peculiar beaked ovary and capsule. These, as well as other features, are shared by *M. gracilenta*, and the two species are believed to be closely related in spite of the different chromosome number, $n = 10$, in *M. gracilenta*. This number, as well as a consistently greater degree of branching, form the basis for the suggestion that *M. gracilenta* stands in an ancestral position to *M. fugax*.

Amongst the various forms of *M. fugax* the following are worthy of mention:

a. A short, large yellow-flowered form, common in the southern Cape and Cape Peninsula, though extending as far north as the Calvinia district.

b. A large, white-flowered form (var. *longifolia*), common along the west coast, with a particularly long leaf, or occasionally with 2 equal or unequal leaves.

c. A late flowering blue form, usually tall and several branched, found from the Cape Peninsula to the Olifants River valley.

d. Dwarf, small white- or blue-flowered forms with either 1 or 2 filiform leaves found along the west coast between Saldanha and Namaqualand; occasionally grading into one or more of the larger forms.

e. A white-flowered form, intermediate between *b* and *d*, throughout Namaqualand.

Other variants have also been noted, but are much more local, and these, together with intermediates between all of the listed forms, make it impossible to subdivide *M. fugax* or to recognize subordinate taxa.

South Africa. cape: 29.17 (Springbok): Steinkopf (BC), *Meyer s.n.* (STE-9090). 33 km N of Springbok (BD), *Mauve 4156* (PRE). Spektakelberg (DA), *Barker 1340, 7423* (both NBG). Near Okiep (DB), *H. Bolus 6616* (BOL). 21 km SW of Springbok (DD), *Acocks 19576* (K, PRE).

30.17 (Hondeklipbaai): 14 km NNW of Garies (BD), *Acocks 14964* (PRE).

30.18 (Kamiesberg): Between Bitterfontein and Garies (C), *Pillans 6346* (BOL); *Leipoldt 3846* (BOL); Mts. near Naries (CA), *H. Bolus 6617* (BOL).

31.18 (Van Rhynsdorp): Van Rhynsdorp (DA), *Kolbe s.n.* (GRA); *Barker 3642* (NBG). 10 km N of Van Rhynsdorp, *Acocks 19499* (M, NBG, PRE). Vredendal commonage, *Hall 3843* (NBG, PRE, STE). N slopes of Giftberg (DC), *Goldblatt 207* (BOL). Nardouw Pass, *Lewis s.n.* (BOL-22205). Zandkraal (DD), *Acocks 14794* (K, PRE).

31.19 (Calvinia): Sandy places near Nieuwoudtville (AC), *Galpin 11128* (K, PRE). Doornbosch (CC), *Hall 3881* (NBG, STE).

32.18 (Clanwilliam): Lamberts Bay (AB), *Henrici 3300* (PRE). Near Olifants R. at Clanwilliam (BB), *Penther 734* (K). Rocky hills, Clanwilliam, *Henrici 2101* (PRE). Pakhuis Pass, *Barker 1999* (NBG); *Compton 9798* (NBG). Zoutkloof, Piketberg district (CD), *Leighton 133* (BOL). 2 km NW of Eendekuil (BB), *Howes 193* (PRE). Hills NW of Moutons Vlei (DC), *Pillans 7398* (BOL). Piketberg (DD), *Barker 2687* (NBG); *Compton 22989* (NBG).

32.19 (Wuppertal): Cedarberg Pass near Algeria (AC), *Goldblatt 3250* (MO).

33.18 (Cape Town): Langebaan (AA), *Lewis s.n.* (BOL). Between Hopefield and Langebaan, *L. Bolus s.n.* (BOL-20339, K). Near Hopefield, *Marloth 8207* (PRE). Groenekloof (AD), *Zeyher 1646* (K, PRE, S). Malmesbury (BC), *Barker 2554* (NBG). 10 km N of Malmesbury, *Goldblatt 3025* (MO, NBG, PRE). Near Sea Point, Cape Town (CD), *Wolley Dod 1611* (BOL). Kirstenbosch, *Barker 2066* (BOL); *Verdoorn s.n.* (PRE). Table Mountain, *Ecklon 823* (PRE-11149).

33.19 (Worcester): Hills near Saron (AA), *Schlechter 10605* (BR, K, PRE, S). Michells Pass (AD), *Schlechter 8966* (GRA). Near French Hoek (CC), *Gillett 1830, 1831* (both STE). 15 km from MacGregor on Bonnievale rd. (DD), *Marsh 806* (PRE, STE).

34.18 (Simonstown): Beyond Simonstown (AB), *Wolley Dod 505* (BOL, K). Fish Hoek, *Wolley Dod 1633* (BOL, K). Olifants Bos (AD), *Barker 3876* (BOL, NBG). Smitswinkel, Cape Peninsula, *Walgate 433* (NBG). Dunes near Strand (BB), *Parker 4141* (BOL, K).

34.19 (Caledon): Caledon (AB), *Gillett 1111* (STE). Onrust R. (AC), *Van Viekerk 300* (BOL). Spes Bona, Genadendal (BA), *Govt. Soil Survey 17* (PRE).

34.20 (Bredasdorp): Near Storms Vlei (AA), *Goldblatt 2923* (MO, PRE). 14 km E of Swellendam (BA), *Story 3090* (PRE). Zoetendals Vlei (CA), *Leipoldt 3559* (PRE).

34.21 (Riversdale): Riversdale (AB), *H. Bolus s.n.* (BOL).

34.22 (Mossel Bay): Mossel Bay (AA), *Burchell 6295* (K). Ruigte Vlei, near Knysna (BB), *Fourcade 1557* (BOL, GRA).

Section 5. **Tubiflora** Goldbl., Ann. Missouri Bot. Gard. 63: 7. 1976. TYPE: *Moraea cooperi* Baker.

Helixyra Salisb., Trans. Hort. Soc. London 1: 305. 1812, nom. nud.
Helixyra Salisb. ex N.E. Br., Trans. Roy. Soc. S. Africa 17: 348. 1929. TYPE: *H. flava* Salisb. = *Moraea longiflora* Ker.

Plants small to medium in size, several to many branched. *Leaves* 2 or more, the lower ± basal, linear, canaliculate. *Stem* subterranean or emergent and flexuose. *Flowers* with tepals united in a perianth tube; *inner tepals* present or entirely lacking. *Capsule* enclosed; *seeds* small, angular. Basic chromosome number $x = 10$.

Distribution: Southwestern Cape, in the Caledon, Worcester, and Stellenbosch districts and in Namaqualand.

Section *Tubiflora* comprises two very unusual species, *Moraea cooperi* and *M. longiflora*, both unique in *Moraea* in having a true perianth tube. *Moraea cooperi* is further unusual in having flowers solitary in each spathe and in lacking inner tepals. The multi-branched habit of *M. cooperi*, its two produced leaves, as well as the karyotype with three long and seven short chromosome pairs, link section *Tubiflora* to section *Moraea*, of which it is regarded as a very specialized offshoot.

The second species of section *Tubiflora*, *M. longiflora*, was assigned by Salisbury in 1812 to the invalidly described *Helixyra*, as *H. flava*. The generic distinction separating *Helixyra* from *Moraea* was the perianth tube, now known also in *M. cooperi*. *Helixyra* was later validated by N. E. Brown and also used as a subgenus of *Moraea* by Baker, but in both cases it was misinterpreted and species

now regarded as belonging to *Gynandriris* were also included. The floral tube in *Gynandriris* differs fundamentally from that of *Helixyra* (i.e., *M. longiflora*) as in the former it is dervied solely from the ovary which has a sterile tubular extension.

21. **Moraea cooperi** Baker, Handbook Irid. 54. 1892. TYPES: South Africa, Cape, Worcester, *Cooper 1661* (K, lectotype); Tulbagh, *H. Bolus 5428* (K, syntype).—FIG. 22C–D.

M. stenocarpa Schlecht., Bot. Jahrb. Syst. 27: 93. 1900. TYPE: South Africa, Cape, between Bains Kloof and Ceres Road, *Schlechter 9082* (B, lectotype; BOL, GRA, MO, PRE, S, SAM, isolectotypes).

Gynandriris stenocarpa (Schlecht.) Foster, Contr. Gray Herb. 127: 47. 1939.

Moraea apetala L. Bol., S. African Gard. 19: 385. 1929. TYPE: South Africa, Cape, Stellenbosch Flats, *Duthie 1770* (BOL, holotype; K, isotype).

Gynandriris apetala (L. Bol.) Foster, Contr. Gray Herb. 127: 48. 1939.

Plants 15–25 cm high, moderately to much branched. *Corm* 1–1.5 cm in diameter; tunics of dark fibers. *Prophylls* brown and fibrous, forming a neck around the stem base. *Leaves* usually 2, linear, canaliculate, the lower basal, exceeding the inflorescence, the upper inserted well above ground. *Stem* flexuose, usually much branched. *Spathes* herbaceous with brown attenuate apices; inner spathe 3–5 cm long, the outer ca. ⅓ the inner. *Flowers* solitary in the spathes, pale yellow, purple veined; tepals united in a tube 1 cm long, the outer tepals 3.3–4.0 cm long, the limb ca. 2 cm long, to 2.0 cm wide, lanceolate, the inner tepals absent. *Filaments* to 6 mm, joined for ca. 2 mm; *anthers* 7–9 mm long. *Style branches* 1.2–1.5 cm long, the crests lanceolate, to 1 cm long. Chromosome number $2n = 20$.

Flowering time: Late September and October, occasionally in November at higher altitudes.

Distribution: Usually on well-watered flats, in the area between Caledon, Stellenbosch and Tulbagh.—FIG. 22.

While its very branched habit and chromosome number of $n = 10$ indicate its basically primitive position in *Moraea*, *M. cooperi* has such unusual features as a perianth tube, only three tepals, and solitary flowers. It is consequently seen as a rather divergent and specialized offshoot of subgenus *Moraea* and has, along with *M. longiflora*, been accorded sectional status. Its karyotype is similar to subgenus *Moraea* and indicates its alliance to this group (Goldblatt 1976a).

Since Baker described *M. cooperi* in 1892, two synonyms have appeared. Evidently both Schlechter (*M. stenocarpa*) and Louisa Bolus (*M. apetala*) did not realize the correct identity of *M. cooperi* (Baker's description is poor and incorrect in some aspects). Foster (1939) believed *M. cooperi* to be a *Gynandriris* owing to its perianth tube and thus transferred it to this genus. The floral tube in *Gynandriris* is, however, derived from a sterile prolongation of the ovary, while *M. cooperi* has a true perianth tube of united tepals, and there is thus no connection between *M. cooperi* and *Gynandriris*.

Moraea cooperi has a rather limited distribution, occurring only in the Caledon, Stellenbosch, and Tulbagh-Worcester districts. It is nowhere common and its usual habitat, fertile, well-watered flat areas, is being brought under intensive

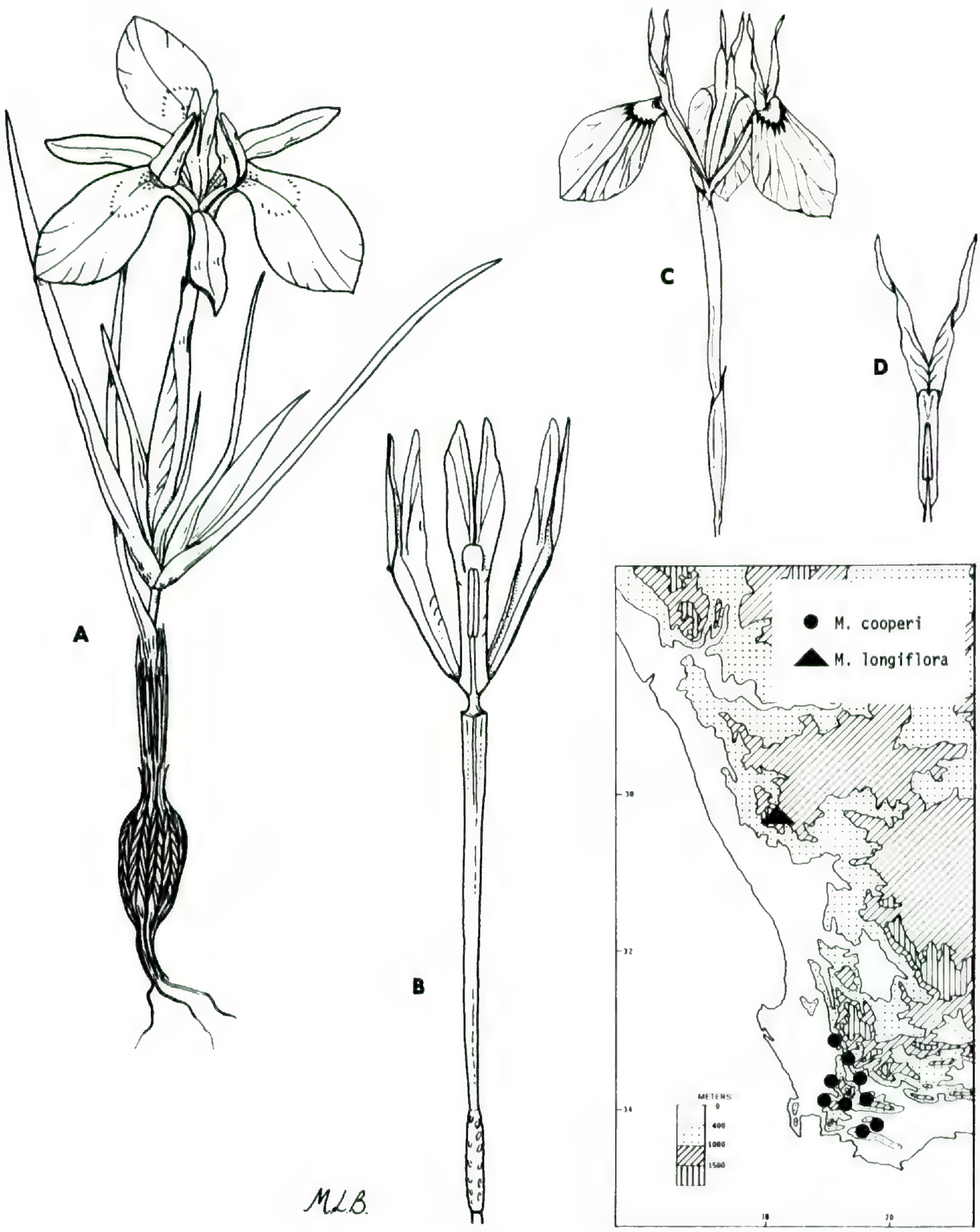


FIGURE 22. Morphology and distribution of *Moraea cooperi* and *M. longiflora*.—A–B. *M. longiflora*—A. Habit (×1.5).—B. Perianth tube, stamens and gynoecium (×2.5).—C–D. *M. cooperi*.—C. Flower (×1.5).—D. Style branch and stamen (×2.5).

agriculture, thus making it increasingly rare. It is notably responsive to fire and is seen most often on recently burnt ground.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Stellenbosch flats (DD), *Duthie 1770* (BOL, K). Banhoek, Stellenbosch, *Stanford s.n.* (BOL). Groot Drakenstein, *Rogers 17919* (BOL).

33.19 (Worcester): Saron (AA), *Lewis s.n.* (BOL). Winterhoek, near Tulbagh, *Bolus*

5284 (BOL, K). Near Tulbagh Waterfall, *Thompson 1524* (STE). Foot of Elands Kloof Mountains (AC), *Stokoe s.n.* (SAM-69629). Ceres Road (Wolseley), *Schlechter 9082* (B, BOL, GRA, K, MO, SAM, PRE). Slanghoek, flats (CA), *Rycroft 2354* (NBG). Du Toits Kloof, foot of Slanghoek Needle, *Esterhuysen 17819* (BOL, NBG, PRE). Darling Bridge, Bains Kloof, *Lewis 1990* (SAM). Pokkraal, near Rawsonville (CB), *Le Roux s.n.* (BOL, PRE-7814). French Hoek above village (CC), *Phillips 1302* (SAM). French Hoek Peak, *Stokoe s.n.* (SAM-58743).

34.19 (Caledon): Foot of Zwartberg (AB), *Guthrie s.n.* (BOL-16923). Roadside S of Caledon, *Goldblatt 441* (BOL). Drayton Siding E of Caledon, *Goldblatt 440* (BOL); *Mauve 4779* (PRE).

Without precise locality: Worcester, *Cooper 1661* (K).

22. **Moraea longiflora** Ker, Bot. Mag. *tab. 712.* 1804. TYPE: Illustration in Bot. Mag. *tab. 712.*—FIG. 22A–B.

Helixyra longiflora (Ker) N.E. Br., Trans. Roy. Soc. S. Africa 17: 349. 1929.
Gynandriris longiflora (Ker) Foster, Contr. Gray Herb. 114: 40. 1936.
Helixyra flava Salisb., Trans. Hort. Soc. London 1: 305. 1812, nom. illeg., superfl. pro *M. longiflora* Ker.

Plants small, ca. 5 cm high with 2–4 branches clustered at ground level. *Corm* spindle shaped, ca. 1 cm wide; tunics dark brown, very hard, reticulate. *Leaves* several, 1 basal, 4–6 cm long, rigid linear-filiform, canaliculate, the other leaves similar, clustered at ground level. *Spathes* herbaceous, 2.5–3 cm long; inner spathe entirely sheathing, the outer somewhat leaflike, sheathing for ca. 5 mm, free in the upper part. *Flowers* yellow with yellow orange nectar guides; tepals united in a tube 2–3 cm long, the outer tepals 2.3–3.0 cm long, the limb to 2 cm long, spreading, the inner tepals 1.7–2.2 cm long, also spreading or becoming reflexed. *Filaments* 5–6 mm, united in the lower third; *anthers* ca. 5 mm long. *Style branches* 1.0–1.2 cm long, the crests to 1 cm long. *Capsule* and *seed* unknown. Chromosome number unknown.

Flowering time: October.

Distribution: Recorded only from the Kamiesberg in Namaqualand where it is very local in moist sandy situations.—FIG. 22.

Moraea longiflora has until very recently been an enigma, no South African plant being known resembling the type which is an excellent illustration in Curtis's *Botanical Magazine*. According to Ker who described it, the species was sent to him by George Hibbert MP, a director of the East India Company and enthusiastic grower of Cape plants, two years after Hibbert himself had flowered it at his garden in Clapham, London. Hibbert had received the corms from the Cape shortly before this, probably in 1800 or 1801. According to the *Hortus Kewensis* ed. 2, which includes *Moraea longiflora*, the corms were collected and sent to Hibbert by James Niven who had in 1798 been employed by Hibbert and sent to collect plants for him in the Cape.

Moraea longiflora remained known only from the painting until 1976 when accompanied by my wife, Margaret, I visited the Kamiesberg rather late in the season, in mid October, in search of corms of various Iridaceae known from the area. Nothing could have been more surprising than the rediscovery of this plant which my wife found and realized was very unusual. The two remarkable features of the plants, a long perianth tube and underground stem, reminded me

of the *Botanical Magazine* plate of *M. longiflora*, and on later examination was found to match it in every detail. It is almost certain that the original collection of *M. longiflora* was made in the Kamiesberg, since, according to Dr. John Rourke, Niven visited the Kamiesberg soon after his arrival in the Cape in 1799 or 1800.

Unusual though the species is, *M. longiflora* bears a passing resemblance to *M. cooperi*, the only other species of *Moraea* with a perianth tube. The two are most likely closely related and have been grouped together in section *Tubiflora*.

SOUTH AFRICA. CAPE: 30.18 (Kamiesberg): E slopes of Rooiberg, near Welcome, 1100 m (AC), *Goldblatt 4317* (K, MO, NBG, PRE, S).

II. Subgenus VISCIRAMOSA

Subgenus **Visciramosa** Goldbl., Ann. Missouri Bot. Gard. 63: 7. 1976. TYPE: *Moraea bituminosa* (L.f.) Ker.

Plants medium to large, several to many branched. *Corm* tunics distinctive, entire and dark brown, with bituminous inner surfaces. *Leaves* 2–3, canaliculate. *Stem* well developed with viscous, sticky nodes, branching repeatedly. *Flowers* with entire, spreading or reflexed tepals. *Style branches* produced and with distinct crests or reduced, without crests and overtopped by anthers. *Capsule* ovoid to clavate; *seeds* angled. Basic chromosome number $x = 10$.

Distribution: Winter rainfall area from Namaqualand in the north to Grahamstown in the east, with a concentration of species in the Cape Town and Caledon districts.

Subgenus *Visciramosa* is a very distinct alliance in *Moraea*. The distinctive corm tunics with their sticky, bituminous surface, the branched axis, and viscous stems, as well as rather short spathes all suggest that the group is only distantly related to other subgenera. The karyotype is unlike that found in any of the other groups with a base number of $x = 10$; the chromosomes grade from large to small without the sharp size differences found in subgenus *Moraea*.

In contrast with the distinctiveness of the subgenus, the five species recognized are closely allied, and differ only in small details. The decision to recognize these five species was governed by the absence of intermediates between taxa, as well as the existence of clearly distinguishable habitats and ranges for each. Vegetative morphology is almost identical, *M. bituminosa* and *M. bulbina* differing primarily in size from *M. viscaria*, *M. inconspicua*, and *M. elsiae*. Flower structure is more variable, and important considerations are length of tepals, their orientation, either spreading or reflexed, and, in the case of *M. elsiae* (and in a form of *M. viscaria*), reduction of style branches and crests.

23. **Moraea bituminosa** (L.f.) Ker, Ann. Bot. (König & Sims) 1: 240. 1805. —FIG. 23A–B.

Iris bituminosa L.f. Suppl.: 98. 1781. Type: South Africa, Cape, "prope Bergrivier, Vierentvingtigrivieren et alibi," *Thunberg s.n.* (Herb. Thunberg 1114, UPS, lectotype).
Vieusseuxia bituminosa (L.f.) Eckl., Top. Verz. 14. 1827.
Moraea viscaria var. *bituminosa* (L.f.) Baker, Flora Cap. 6: 15. 1896.

Plants 25–50 cm high, flexuously branched. *Corms* 1.5–2.0 cm in diameter; tunics dark brown, sticky and bituminous on the inner surfaces. *Leaves* 2, the

lower basal, the upper attached to the lowest aerial node, linear, glabrous, falcate. *Stems* repeatedly branched, viscous below the nodes. *Spathes* herbaceous, becoming dry and conspicuously nerved with age, the apices obtuse, brown, occasionally lacerated, 2.5–4.0 cm long, subequal or the outer only slightly shorter. *Flowers* bright yellow; outer tepals 2–3 cm long, spreading or reflexed to ca. 45°; inner tepals 2–2.5 cm long, also reflexed. *Filaments* 5–7 mm long, free in the upper 1–2 mm; *anthers* 5–7 mm long. *Style branches* ca. 6 mm long, the crests to 8 mm, lanceolate. *Capsule* ovoid, 1.0–1.3 mm long; *seeds* angled. Chromosome number $2n = 20$.

Flowering time: October to mid December.

Distribution: Sandstone or shale slopes, mainly in the southwest, from Bredasdorp to Porterville.—FIG. 23.

Moraea bituminosa is typified by a Thunberg specimen, also illustrated in the *Dissertatio de Iride*, which is said to have been collected in the Twenty-four Rivers area south of Porterville. Both the coiled leaves and early flowering time (described as September by Thunberg) are unusual. Other features are, however, in keeping with the association of the large-flowered, bright yellow species of subgenus *Visciramosa*, from the southwestern Cape with the Thunberg collection.

It can readily be distinguished from its allies by its large flower with spreading to partially reflexed tepals and by the large obtuse spathes, 2.5–4 cm long. Confusion between *M. bituminosa* and *M. bubalina* is possible as the latter has equally large tepals and spathes. The spathes of *M. bubalina* are however distinctly acute and in addition this species, from the dry areas in the Clanwilliam-Van Rhynsdorp area, has dull buff- to khaki-colored flowers.

Moraea bituminosa is frequently found on sandy soils, but has been collected on the mixed clay-sand of lower mountain slopes. It is common on flats and slopes between Bredasdorp in the southeast and the Wellington-Tulbagh area to the north. The large clear yellow flowers open after midday and last until about sunset.

Though occasionally treated as a variety of *M. inconspicua* (as *M. viscaria*), (Baker, 1896), *M. bituminosa* is quite distinct morphologically and to a lesser extent ecologically from the other members of the subgenus *Visciramosa*.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Blinkwater Ravine, Cape Peninsula (CD), *Cassidy 72, 87* (both NBG). Lions Head, *Compton 12545* (NBG). Wynberg Hill, *Pillans 10354* (BR, MO). Above Bakoven, Camps Bay, *Barker 3234* (NBG).

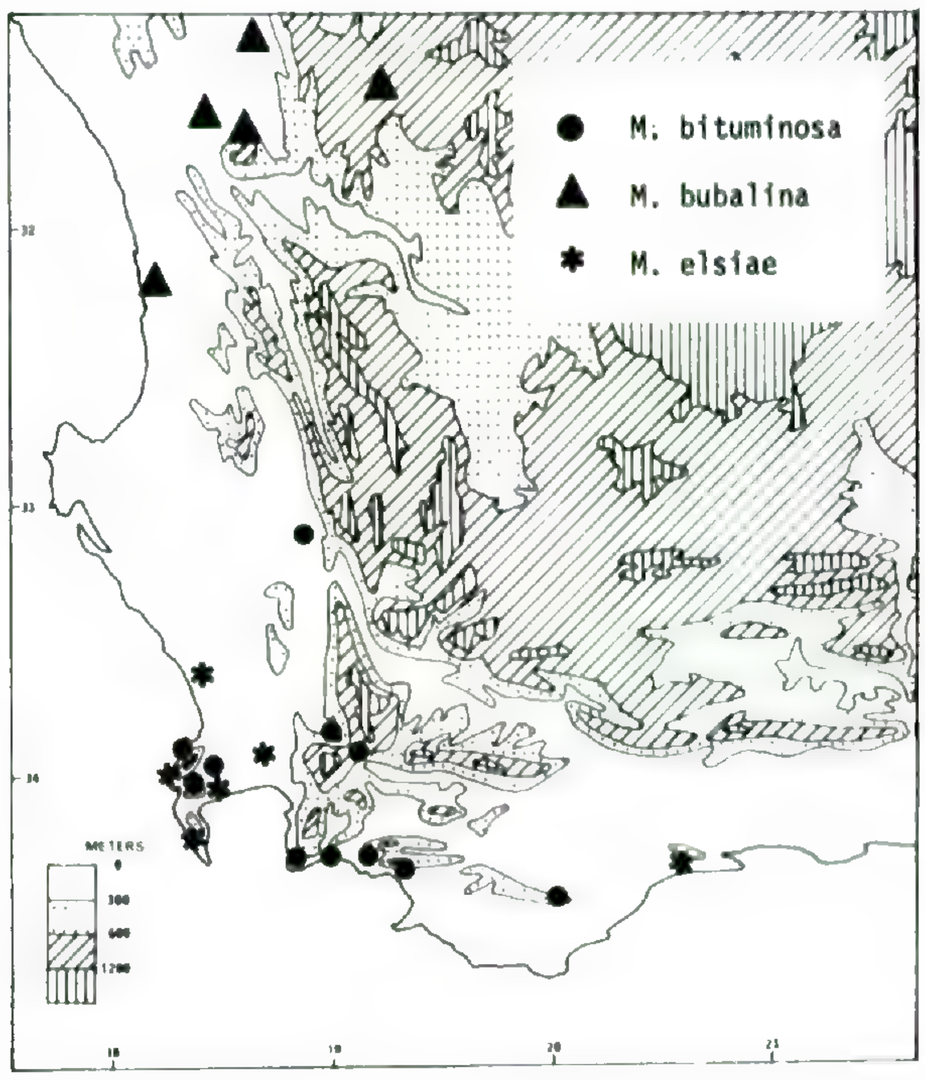
33.19 (Worcester): Twenty-four Rivers (AA), *Thunberg s.n.* (UPS).

34.18 (Simonstown): Constantia Nek, Cape Peninsula (AB), *Goldblatt 392* (BOL). Bergvliet, Cape Peninsula, *Purcell s.n.* (BOL-16383). Chapmans Peak, *Compton 15398* (NBG). Dieprivier, Cape Peninsula, *Marloth 7210A, 7211* (both PRE). Buffels River, Hangklip (BD), *Barker 3918* (NBG). Disa Kloof, Bettys Bay, *Ebersohn s.n.* (NBG). Palmiet River mouth, *Barker 1342* (NBG).

34.19 (Caledon): Sandy slopes above Hermanus (AC), *Goldblatt 3325* (MO). Caledon (BA), *Penther 761* (S).

34.20 (Bredasdorp): Mountains above Bredasdorp (CA), *Barker 10853* (NBG).

24. **Moraea bubalina** Goldbl., sp. nov. TYPE: South Africa, Cape, Zandkraal, Van Rhynsdorp, *Barker 5667* (NBG, holotype).



MLB

FIGURE 23. Distribution of *Moraea bituminosa*, *M. bubalina*, and *M. elsiae*, and floral morphology of *M. bituminosa* and *M. elsiae*.—A–B. *M. bituminosa*.—A. Flowering branch (life size).—B. Style branch and stamen (×2).—C–E. *M. elsiae*.—C. Flowering branch (life size).—D. Stamens and style branches (×4).—E. Style branch and stigma (×8).

Planta multiramosa, 20–45 cm alta, viscosa sub nodis. *Spathae* 2.8–3.6 cm longae, herbaceae, acutae. *Flores* bubalini ad pallidi-brunnei; tepala exteriora 2.2–2.8 cm longa, reflexa ad ca. 45°; tepala interiora breviora, reflexa. *Rami styli* producti.

Plants similar to *Moraea bituminosa* but frequently with more than 2 leaves. *Spathes* 2.8–3.6 cm long, herbaceous, acute. *Flowers* buff to light brown; outer tepals 2.2–2.8 cm long, reflexed to ca. 45°; inner tepals shorter, also reflexed. *Filaments* ca. 8 mm, free in the upper ⅓; *anthers* 4 mm long. *Style branches* ca. 7 mm long, crests 2–3 mm. *Capsule* not known. Chromosome number not known.

Flowering time: September to October.

Distribution: Clay gravel flats and slopes in the Calvinia, Clanwilliam, and Van Rhynsdorp districts.—Fig. 23.

Moraea bubalina is distinct in subgenus *Visciramosa* in having acute inflorescence spathes and frequently more than two leaves. The large buff to brown flowers and spathes exceeding 2.7 cm separate it from the more common *M. inconspicua* which occurs in the same area. In overall size it most resembles *M. bituminosa*, but the buff brown flowers, as well as the acute spathes, make any confusion between these two species unlikely.

Though it has seldom been collected, *M. bubalina* is more common than the record suggests, and I have observed it at several places in the Clanwilliam, Van Rhynsdorp, and Calvinia districts. The paucity of collections may be explained to some extent by the fact that flowers open only after midday and are inconspicuous owing to their dull color.

South Africa. cape: 31.18 (Van Rhynsdorp): Zandkraal (DA), *Barker 5667* (NBG). Wiedouw River, *Goldblatt 3075B* (MO).
31.19 (Calvinia): Plaatberg farm (DA), *Acocks 18613* (K, M, PRE).
32.18 (Clanwilliam): Near Lamberts Bay (AA), *Loubser s.n.* (BOL).

25. **Moraea viscaria** (L.f.) Ker, Ann. Bot. (König & Sims) 1: 240. 1805, as to name only, not to plant intended.—Fig. 24A–B.

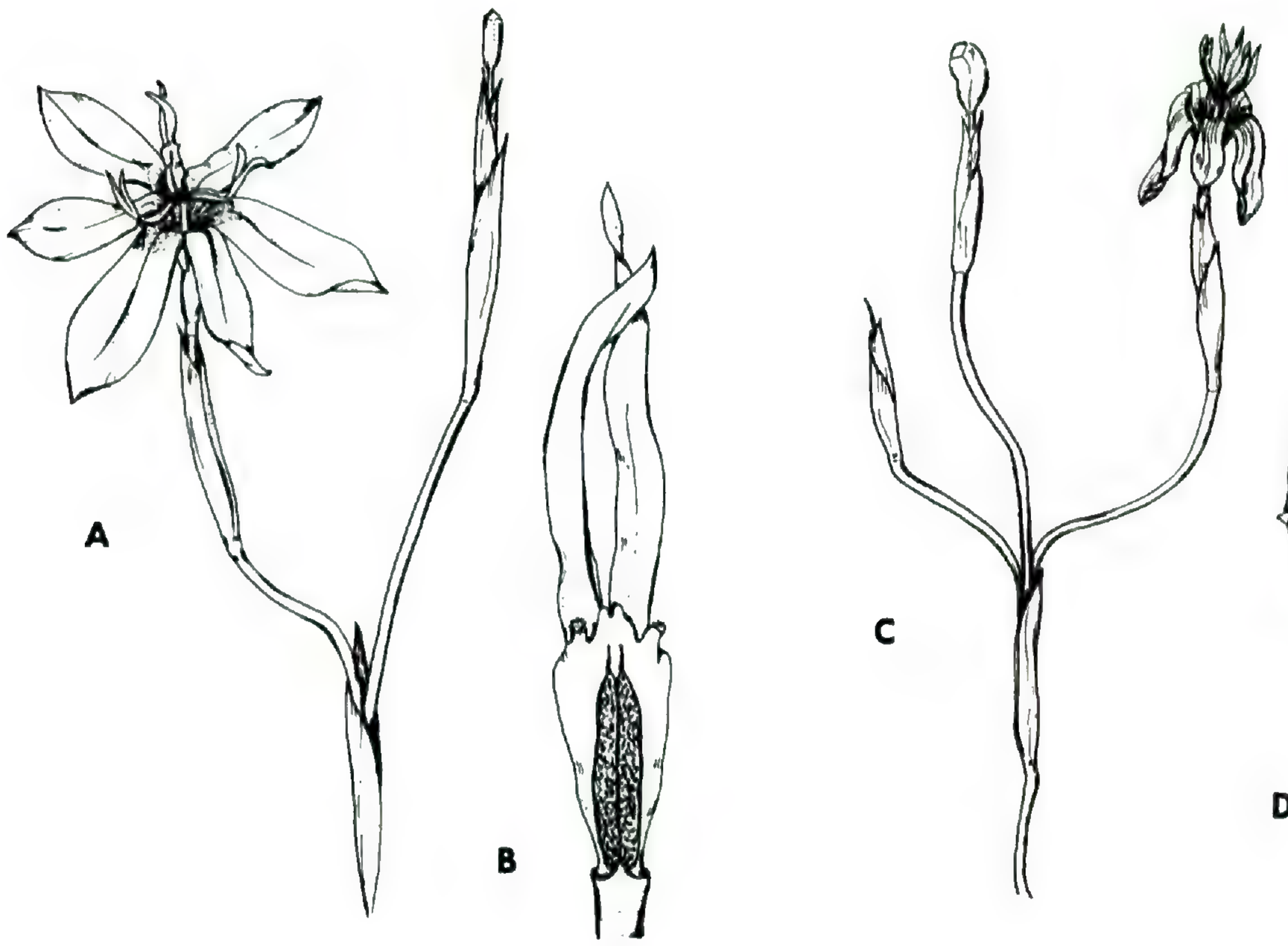
Iris viscaria L.f., Suppl. Pl. 98. 1781. type: South Africa, Cape, "Lospers farm," Saldanha district, *Thunberg s.n.* (Herb. Thunb. 1200, UPS, holotype).
Vieusseuxia viscaria (L.f.) Eckl., Top. Verz. 12. 1827.
Moraea odorata Lewis, J. S. African Bot. 7: 53. 1941. type: South Africa, Cape, Rondebosch Common, *Barnard s.n.* (BOL-20341, holotype; PRE, SAM, isotypes).

Plants similar to *Moraea bituminosa* in habit, 20–45 cm high. *Spathes* 1.8–2.4 cm long. *Flowers* white, sometimes flushed with purple, sweetly scented; outer tepals 1.5–2.3 cm long, spreading to slightly reflexed; inner tepals 1.4–2.0 cm long. *Filaments* 5–6 mm, free near the apex only; *anthers* 4–5 mm long, acuminate, red. *Style branches* to 5 mm, the crests to 6 mm or occasionally reduced to 1 mm. *Capsule* broadly ovoid, 7–10 mm long. Chromosome number $2n = 20$.

Flowering time: Late September to October in the Saldanha area, elsewhere November to December.

Distribution: Sandy flats between Cape Agulhas in the east and Saldanha Bay in the north.—Fig. 24.

Though first described by the younger Linnaeus (who placed it in *Iris*), *Moraea viscaria* can only be identified from Thunberg's own description pub-



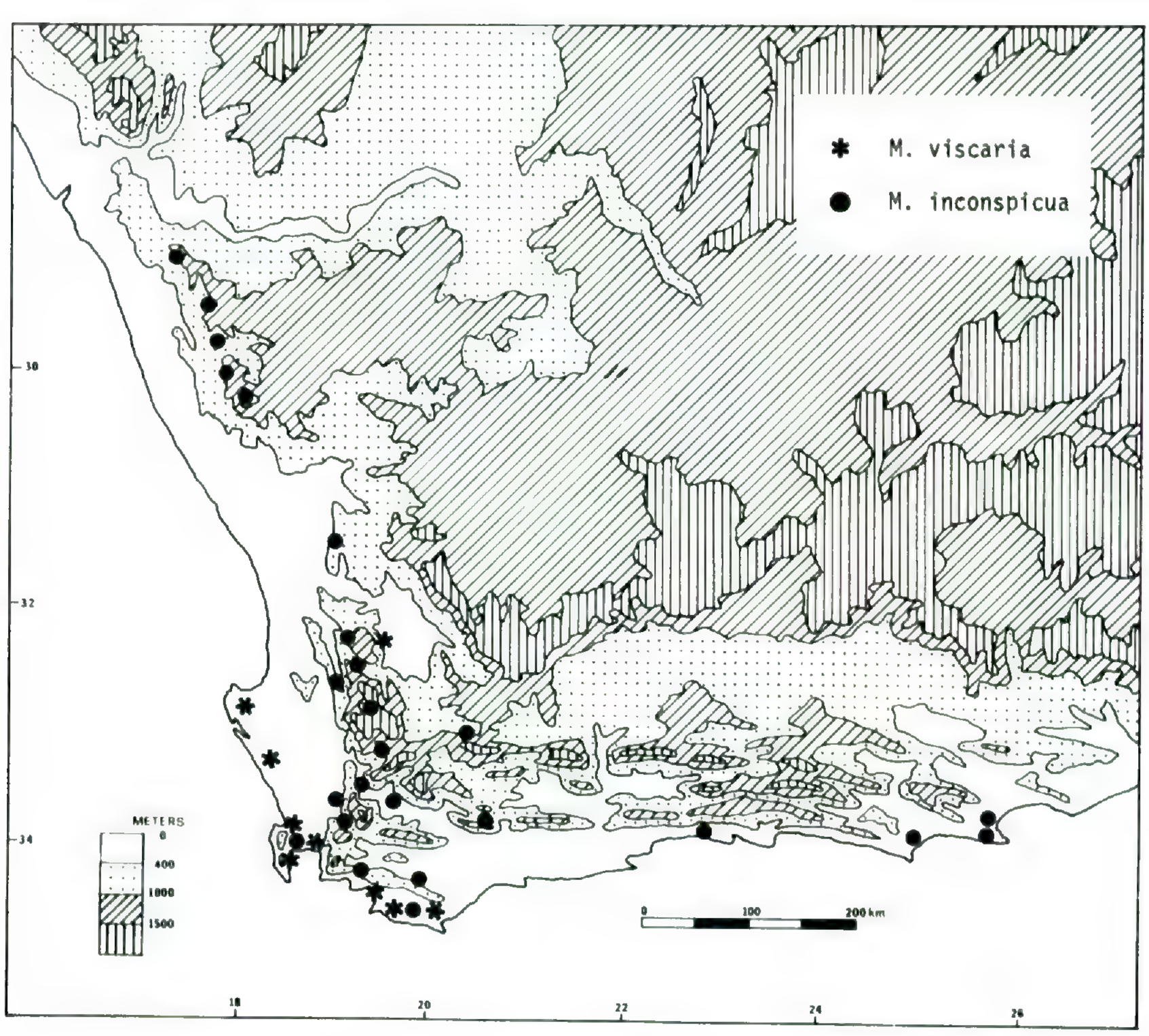


FIGURE 24. Distribution and floral morphology of *Moraea viscaria* and *M. inconspicua*. —A–B. *M. viscaria*.—A. Flowering branch (life size).—B. Style branch and anther (×4). —C–D. *M. inconspicua*.—C. Flowering branch (life size).—D. Stamens and style branches (×3).

lished a year later, and by his specimen collected in the Saldanha Bay district. Thunberg clearly described his plant as white flowered, flushed with purple, indicating that it is very likely conspecific with the plant described later by Lewis (in 1941) as *M. odorata*. After careful consideration of the description, it has become clear that the name *M. viscaria* must be applied to the white-flowered and usually scented plant which Lewis called *M. odorata*, and not to the small yellow- to brown-flowered species known by this name since Ker illustrated it in the *Botanical Magazine* in 1802.

This interpretation of the identity of *M. viscaria*, based on color, is supported by the recorded habitat—"in arenosis"—and, since the tepals are not described by Thunberg as reflexed, as for example in *M. bituminosa*, they are by inference spreading. Both facts are consistent with the belief that *M. viscaria* is conspecific with *M. odorata* and is not the same as the plant that has been associated with the name *M. odorata* since 1802. The latter, redescribed here as *M. inconspicua*, apparently always has strongly reflexed tepals and rarely grows in sandy situations. Moreover, *M. inconspicua* is not known from the Saldanha district, while specimens such as *Barker 8072*, previously assigned to *M. odorata*, do occur here.

Moraea viscaria has been recorded all along the southwestern Cape coast, from Saldanha in the north to Agulhas in the east. It invariably grows at low altitudes, often close to the sea, and in sandy soil. The white flowers open between 2 and 3 P.M. and last till evening. Most forms are very sweetly scented. Occasionally plants, and probably local populations, lack style crests and have, in general, *Homeria*-like flowers. These are not given taxonomic recognition as their characteristics are otherwise typical of *M. viscaria*.

The white color, scent, and outspread tepals all distinguish *M. viscaria* from its allies, *M. inconspicua* and *M. elsiae*, which also have small flowers and short inflorescence spathes.

SOUTH AFRICA. CAPE: 32.17 (Vredenburg): Granite outcrops near Vredenburg (DD), *Barker 8072* (NBG); *Lewis s.n.* (SAM-65685).

33.18 (Cape Town): Darling, flora reserve (AD), *Rycroft 2013* (NBG). Camp Ground, Cape Peninsula (CD), *Barnard s.n.* (BOL-20341, PRE, SAM). Milnerton, Cape Peninsula, *Salter 8705* (BOL, K, NBG, SAM).

34.18 (Simonstown): Cape Flats (BA), *Salter 8707* (SAM). Isoetes Vlei, *Barker 10592* (NBG, S, STE). Retreat, Cape Peninsula, (AB), *Salter 8724* (SAM), *4005* (K).

34.19 (Caledon): Near Hermanus (AC), *Loubser 2141* (NBG); *Leighton 365* (BOL, PRE). Onrust River, *Van Niekerk 304* (BOL). Hawston, *Schlechter 1615* (PRE). Near Elim (DA), *Barnard s.n.* (BOL). Ratelrivier, near Die Dam, *Goldblatt 478* (BOL). 10 km NE of Die Dam, *Acocks 23195* (PRE).

26. **Moraea inconspicua** Goldbl., sp. nov. TYPE: South Africa, Cape, Wilderness, *Van Niekerk 181* (BOL, holotype; PRE, isotype).—FIG. 24C–D.

Moraea viscaria sensu Ker, Bot. Mag. *tab.* 587. 1802; Baker, Fl. Cap. 6: 15. 1896, excl. vars; Lewis, Fl. Cape Pen. 229. 1950.

Planta multiramosa, 20–45 cm alta, viscosa sub nodis. *Spathae* 1.8–2.6 cm longae, herbaceae, obtusae, apicis brunneis. *Flores* flavi ad brunnei; tepala exteriora 1.3–1.8 cm longa, tota reflexa; tepala interiora similes sed breviores. *Filamenta* libera, contigua vel connata. *Rami styli* producti, cristae 3–6 mm longae.

Plants similar to *Moraea bituminosa*, 20–45 cm high. *Spathes* 1.8–2.6 cm long. *Flowers* yellow to brown; outer tepals 1.3–1.8 cm long, reflexed to 90° or more;

inner tepals 1.2–1.7 cm long, also reflexed. *Filaments* 5–6 mm long, free but contiguous, or united in part; *anthers* 3–4 mm long. *Style branches* ca. 5 mm long, the crests 3–6 mm long. *Capsule* broadly ovate, 7–10 mm long. Chromosome number $2n = 20$.

Flowering time: September to December (January).

Distribution: Throughout the winter rainfall area, usually in dry, exposed habitats.—FIG. 24.

Moraea inconspicua is one of the most widespread species in subgenus *Vis-ciramosa* and is found throughout the Cape winter rainfall area from Namaqualand in the north to the Port Elizabeth district. Over this range it occurs in a variety of habitats: dry stony hills near Springbok to sandy soils in the sandveld, near Darling, to clay flats and slopes from the Caledon district eastwards. Flower color is variable with both brown and clear yellow being common, while white is also known. The leaves are usually straight and more or less erect, but plants from Namaqualand have characteristically spirally coiled leaves. *Moraea inconspicua* is distinguished by its short spathes, less than 2.6 cm long, and small flower, with completely reflexed tepals. A white form occurring in the Bidouw valley near Clanwilliam is tentatively assigned to *M. inconspicua*, though details of tepal orientation are not known.

Moraea inconspicua has been known since Ker described the plant illustrated in *Botanical Magazine* in 1803, but the name associated with it, *M. viscaria*, based on Thunberg and the younger Linnaeus's *Iris viscaria* is now believed to have been misapplied (see discussion under *M. viscaria*). *Iris viscaria* is here regarded as the earliest name for what has until now been called *M. odorata*, a white-flowered species with spreading tepals. The new name *M. inconspicua* is thus assigned to Ker's plant in this treatment.

SOUTH AFRICA. CAPE: 29.17 (Springbok): Steinkopf (BC), *Herre s.n.* (BOL). Hills E of Nababeep (DB), *Goldblatt 3054* (MO, NBG).

31.19 (Calvinia): Moist sandy places near Nieuwoudtville (AC), *Galpin s.n.* (BOL, K, PRE).

32.19 (Wuppertal): Juriesberg, Cedarberg (AC), *Bond 1400* (NBG). Middelberg, Cedarberg, *Esterhysen 7234* (BOL). Near Warmbaths, Olifants River valley (CC), *L. Bolus s.n.* (BOL-20322, K, PRE). Wagebooms River, Cold Bokkeveld, *Schlechter 10703* (GRA, K, PRE).

33.18 (Cape Town): Stellenbosch flats (DD), *Garside 1122* (K). Bottelary road, *Acocks 3672* (S).

33.19 (Worcester): Romans River (AC), *Bond 147* (NBG). Du Toit's Kloof (CA), *Esterhuysen 17761* (BOL, NBG, PRE). Karoo Garden, Worcester (CB), *Olivier 102* (PRE). French Hoek (CC), *Schlechter 9350* (BR, K, MO, PRE). Bethlehem farm, Pniel, *Wasserfall 716* (NBG); *Esterhuysen 9555* (BOL, PRE). Lower slopes, Naudesberg Koo (DA), *Lewis 5693* (NBG).

33.20 (Montagu): Cabidu, Laingsburg district, *Barker 6767* (NBG).

33.22 (Oudtshoorn): Wilderness (DC), *Van Niekerk 181* (BOL, PRE).

33.24 (Steytlerville): Near Gamtoos River (DD), *Barker 6903* (NBG).

33.25 (Port Elizabeth): Walmer, Port Elizabeth (DC), *Paterson 382* (BOL); *Bokelman 4* (NBG). Baakens River, *Long 484* (GRA, K, PRE).

34.18 (Simonstown): Dieprivier, Cape Peninsula (AB), *Marloth 7210, 7393* (PRE). Bergvliet, gravel soils, *Purcell s.n.* (SAM-90063-5).

34.19 (Caledon): Between Bot River and Hawston (AC), *Goldblatt 3300* (MO). Fairfield (BC), *Acocks 22929* (K, PRE). Near Elim, (DA), *H. Bolus s.n.* (BOL).

27. **Moraea elsiae** Goldbl., Ann. Missouri Bot. Gard. 63: 18. 1976, nom. nov. pro *Homeria simulans* Baker. TYPE: As for *H. simulans*.—FIG. 23C–E.

Homeria simulans Baker, Fl. Cap. 6: 529. 1896. TYPE: South Africa, Cape, sandy places near Kenilworth, *Bolus 7931* (BOL, lectotype; K, MO isolectotypes).

Plants similar to *Moraea bituminosa* in habit, 20–40 cm high. *Spathes* 1.9–3.0 cm long. *Flowers* bright yellow; tepals reflexed to ca. 45°. The outer 1.5–2.2 cm long, ca. 9 mm wide, the inner somewhat smaller, 1.4–1.9 cm long. *Filaments* 4–7 mm long, partly united; *anthers* 3–4 mm long. *Style branches* 3–4 mm long, the crests not produced. *Capsule* ovoid, to 1 cm long. Chromosome number $2n = 20$.

Flowering time: November to December (January).

Distribution: Cape Peninsula and vicinity east to the Bredasdorp district, usually on sandy flats.—FIG. 23.

Although *Moraea elsiae*, known until recently as *Homeria simulans*, has a flower typical of the genus *Homeria*, with reduced style branches which lack crests entirely, its vegetative structure is so strikingly like the species of *Moraea* subgenus *Visciramosa* that its close relationship with this alliance is self evident. The morphological similarities are fully confirmed by the cytology, *M. elsiae* having a diploid number of $2n = 20$ and a karyotype exactly like that in other members of subgenus *Visciramosa*. The karyotype in *Homeria*, on the other hand, is very different, with a base number of $x = 6$.

Homeria simulans was only recently transferred to *Moraea* (Goldblatt, 1976a) in which genus a new name was needed; the alternative, leaving this species in *Homeria* would have made this genus clearly polyphyletic, a quite unacceptable situation. The way in which the style in *M. elsiae* and in *Homeria* has been reduced is exactly the same, and must be regarded as an example of morphological convergence.

Moraea elsiae is relatively rare, though it has been found in several places on the Cape Peninsula. Its range extends across the Cape flats and further east with an isolated record from the Potteberg flats near Bredasdorp. It is very like its allies, *M. viscaria* and *M. inconspicua*, possessing spathes and flowers of a similar size. The absence of style crests and spreading to slightly reflexed tepals, distinguish it from *M. inconspicua*, while its yellow color and lack of scent distinguish it from those forms of *M. viscaria* which also lack style crests.

SOUTH AFRICA. CAPE: 33.18. (Cape Town): Between Mamre and Melkbos Strand (CB), *L. Bolus s.n.* (BOL-19970, K). Blinkwater, Cape Peninsula (CD), *Barker 7182* (NBG). Flats at Sherwood, Kenilworth, *H. Bolus 7931* (BOL, K, MO, PRE). Kenilworth racecourse *Esterhuysen 32358* (BOL). Langverwacht, Kuils River (DC), *Oliver 4793* (STE).

34.18 (Simonstown): Dieprivier, Cape Peninsula (AB), *Marloth 7211A, 7302* (both PRE). Near the railway at Retreat, Cape Peninsula, *Wolley Dod 3654* (BOL, K). Cirkels vlei, Cape Point Reserve, (AD), *Barker 3966* (NBG). Olifantsbosch, *Salter 2893* (BOL).

34.20 (Bredasdorp): Potteberg flats (BC), *Barker 8452* (NBG).

III. Subgenus MONOCEPHALAE

Subgenus **Monocephalae** (Baker) Goldbl. Ann. Missouri Bot. Gard. 63: 7. 1976.

TYPE: *Moraea angusta* (Thunb.) Ker.

Moraea subgenus *Moraea* [sect.] *Monocephalae* Baker, Fl. Cap. 6: 11. 1896, pro parte.

Plants medium, unbranched. *Corm* tunics brown, soft textured, the inner layers ± entire, the outer fibrous. *Leaf* solitary, terete, inserted above ground level. *Stem* erect, the nodes often viscous. *Flowers* large, with erect or reflexed, entire inner tepals. *Ovary* distinctly 3-winged. *Capsule* clavate; *seeds* large, flat, discoid. Basic chromosome number $x = 10$.

Distribution: Southwestern Cape, extending as far north as Nieuwoudtville and as far east as Knysna.

Subgenus *Monocephalae* is a very isolated and morphologically distinct group in *Moraea*. While it has a basic chromosome number of $x = 10$, characteristic also of subgenus *Moraea*, it lacks the distinctive karyotype of large and very small chromosomes found in subgenus *Moraea*. The chromosomes grade from large to small with no sharp differences in size, a feature also of subgenus *Visciramosa*, which has a base number of $x = 10$, and possibly this is indicative of a mutual relationship. The differences between these two subgenera are, however, considerable and preclude the possibility of any close relationship between them. Similarities extend no further than the common characteristic of obtuse bracts and spathes and stickiness on parts of the stem, which is confined to the nodes in some species of subgenus *Monocephalae* while extending along the entire stem in subgenus *Visciramosa*. Differences between the two subgenera are more significant, with subgenus *Monocephalae* having a solitary leaf, unbranched axis, and flat discoid seeds, in contrast to the two or three leaves, the branched axis and small angled seeds of subgenus *Visciramosa*.

Similarity of the seeds of subgenus *Monocephalae* to those found in subgenus *Grandiflora* is striking and this character, as well as the unbranched axis and single leaf, led to Baker's belief that the two were closely related. Other morphological features are so different, that, together with cytology—subgenus *Grandiflora* having a base number of $x = 6$—it seems that the similarities are the result of convergent evolution.

The three species which are recognized in subgenus *Monocephalae* are very similar and consequently difficult to distinguish, and were in fact regarded as a single entity until quite recently.

28. **Moraea angusta** (Thunb.) Ker, Ann. Bot. (König & Sims) 1: 240. 1805; Baker, Fl. Cap. 6: 13. 1896, pro parte.—FIG. 25A–C.

Iris angusta Thunb., Diss. Irid., no. 28. 1782. TYPE: South Africa, Cape, slopes below Devils Peak and Lions Head, Cape Peninsula, *Thunberg s.n.* (Herb. Thunberg 1108, UPS, lectotype).

Moraea obtusa N.E. Br., Bull. Misc. Inform. 1931: 195. 1931. TYPE: South Africa, Cape, marsh at Crawford, Cape flats, *Weintraub sub Moss 18185* (K, BM).

Plants medium in size, 20–40 cm high, solitary, unbranched. *Corms* 1–2 cm in diameter; tunics pale to dark brown, soft textured, the innermost layers ± entire, the outer becoming vertically split, and eventually fibrous. *Leaf* solitary, inserted shortly above ground level, usually rigid and exceeding the inflorescence, terete. *Stem* erect, unbranched, bearing 1 or 2 bract leaves; nodes either smooth or viscous. *Spathes* herbaceous, dark green, the upper margins brown, usually

truncate or obtuse at the apex; inner spathe 6–8 cm long, the outer ca. half the inner. *Flowers* pale yellow, translucent, occasionally pale grey blue, veined purplish below, the nectar guide clear yellow; outer tepals 3–5 cm long, the limb ca. ⅔ the claw; inner tepals 2.5–3.5 cm long, erect, often becoming reflexed at maturity. *Filaments* 5–12 mm long, free almost to the base (joined ca. 1 mm); *anthers* 7–10 mm, the pollen usually orange red, rarely yellow. *Style branches* 11–20 mm long, the crests 13–23 mm, equal or exceeding the style branch. *Capsules* cylindrical, somewhat 3-lobed, 1.5–2 cm long; *seeds* large, flat, disclike. Chromosome number $2n = 20$.

Flowering time: Late August to November.

Distribution: Flats and slopes often in sand, from the Cedarberg in the north to Knysna in the east.—Fig. 25.

Lewis (1949) decided, after careful examination of specimens assigned to *Moraea angusta*, that this actually comprised three species, and she accordingly recognized two new species, *M. neglecta* and *M. anomala*. Although I entertained considerable doubts about the validity of these segregated species, a detailed study of living populations and of herbarium material confirmed Lewis's treatment. In every living population encountered it has been easy to decide which of the three taxa was present, and no significant variability was found within any population. Carefully prepared herbarium specimens can also be readily determined, though in the absence of details of flower color and form, difficulties do arise that are not always fully resolved by measurement.

Important differences between *M. angusta* and its two close allies are given in Table 3. In the vegetative state accurate determination is often impossible and dry flowering material must be measured with care. Fresh flowering material is, however, easy to recognize by flower color and size, nature of the nectar guide, and pollen color. The only reliable characters in dried material are the relative lengths of the style branch and crests, and the degree to which the filaments are united. Both *M. angusta* and *M. neglecta* have filaments free almost to the base, while in *M. anomala* they are united for at least 2 mm and ¼–½ their length. The style crests are narrow and usually exceed a short style branch in *M. angusta* and *M. anomala*, while in *M. neglecta* the style branch is longer than the crest.

One of the difficulties in accepting the validity of all three species in section *Monocephalae* is the absence of any clear differences in geographic range. *Moraea neglecta* extends furthest north to Nieuwoudtville and eastwards as far as the Caledon district; *M. anomala* and *M. angusta* share the same range, extending in the north only to the Cedarberg, but somewhat further east than *M. neglecta* to Swellendam, with *M. angusta* being recorded as far as Knysna.

Habitat differences are also not very marked but the following differences are indicated. *Moraea anomala* is most frequently found on clay soils, notably the shale band of the Cedarberg and Du Toits Kloof Mountains. In contrast, *M. neglecta* is most often encountered on sandy flats, often near the coast. *Moraea angusta* is usually found on lower mountain slopes in a sandy or rocky soil. Though these habitats are not always clear cut, it seems likely that the three species do indeed have subtly different ecological preferences.

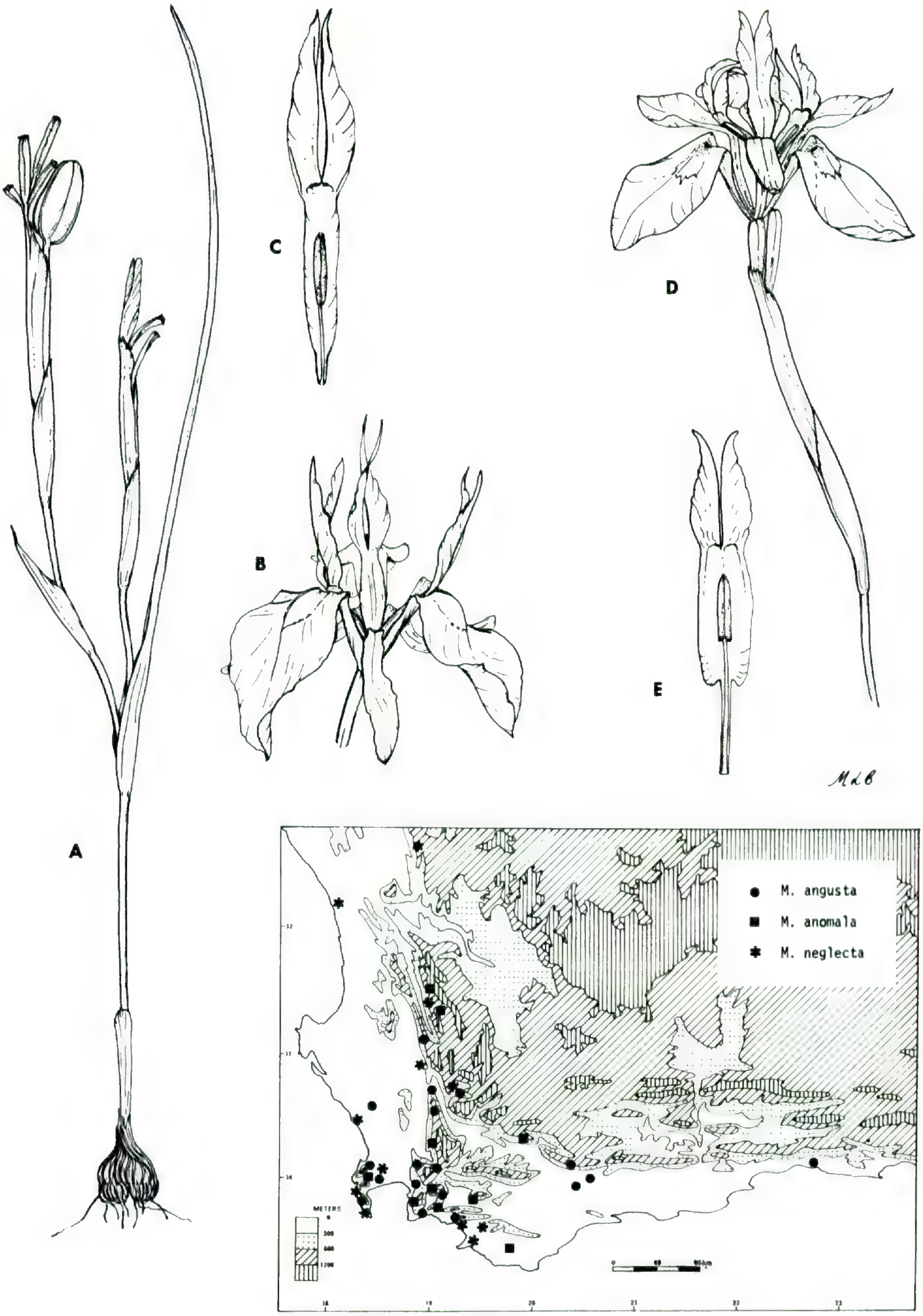


FIGURE 25. *Moraea* subgenus *Monocephalae*: distribution and morphology.—A–C. *M. angusta*.—A. Habit (×0.5).—B. Flower (life size).—C. Stamen and style branch (×1.5).—D–E. *M. anomala*.—D. Flower (life size).—E. Stamen and style branch (×1.5).

TABLE 3. Summary of morphological differences between *Moraea angusta*, *M. anomala* and *M. neglecta*.

Character	*M. angusta*	*M. neglecta*	*M. anomala*
Flower color	Pale translucent yellow, occasionally pale blue	Deep yellow	Pale yellow
Nectar guide	Clear deep yellow	Dotted black lines at the base of the limb	Clear deep yellow
Flower texture	Delicate	Firm	± delicate
Pollen color	Red	Yellow	Usually red
Node condition	Sticky or smooth	Sticky	Smooth
Sheathing leaf number	1 or 2	1	2
Ratio of style crest/style branch	1 or greater	1 or less	Varied
Union of filaments	Ca. 1 mm	Ca. 1 mm	2–7 mm (¼–½ the length)

SOUTH AFRICA. CAPE: 32.19 (Wuppertal): Porterville Mountains (CC), *Thompson 1480* (STE).

33.18 (Cape Town): Mamre Road, 45 km N of Cape Town (BC), *Barker 4096* (NBG). Block House, Camps Bay (CD), *Marloth 465* (PRE). Near Herbarium, Kirstenbosch, *Barker 4790* (NBG). Jakkals Vlei, Jonkershoek (DD), *Taylor 5476* (PRE).

33.19 (Worcester): Tulbagh waterfall (AC), *Schlechter 9005* (K, PRE). Base of mountains, Ceres (AD), *Marloth 6150* (PRE). Wolwekloof, Bains Kloof Mountains (CA), *Barker 4233* (NBG). French Hoek (CC), *Barker 4123* (NBG).

33.20 (Montagu): Below 10 O'Clock Peak (BD), *Wurts 443* (NBG).

34.18 (Simonstown): Suurdam, Cape Point Nature Reserve (AD), *Taylor 7354* (K, PRE, STE). Marsh, Crawford (BA), *Weintraub sub Moss 18185* (K). Sir Lowrys Pass (BB), *Goldblatt 3018* (MO, PRE); *Marloth 4564* (PRE).

34.19 (Caledon): Elgin (AA), *Johns s.n.* (NBG-58650). Top of Houw Hoek Pass, *Lewis 5315* (NBG); *Goldblatt 3292* (MO, NBG, PRE, S). Paardeberg, Palmiet River mouth (AC), *Grobler 77* (STE).

34.20 (Bredasdorp): Bontebok Park, Swellendam (AB), *Liebenberg 6587* (PRE). 7 km E of Swellendam (BA), *Mauve 4771* (PRE).

34.22 (Knysna): Bank of Knysna River above bridge (BB), *Galpin 4642* (K, PRE).

29. **Moraea anomala** Lewis, J. S. African Bot. 15: 119. 1949. TYPE: South Africa, Cape, Houw Hoek Pass, Caledon district, *Lewis s.n.* (SAM-58100, holotype).—FIG. 25D–E.

Plants similar to *Moraea angusta*. Stem bearing 2 bract leaves; nodes not viscous. *Spathes* 4.5–6 cm long. *Flowers* pale yellow with distinct darker nectar guide; outer tepals 3–4.5 cm long, the limb ± equal to the claw; inner tepals 2.5–3.5 cm long, erect, becoming reflexed at maturity. *Filaments* 6–14 mm long, united for at least 2 mm and usually ⅓–½ their length; *anthers* 4–8 mm long, the pollen usually red. *Style branches* 9–14 mm long, the crests ± equal in length or somewhat exceeding the branches, 10–15 mm long. *Capsule* and *seeds* as in *M. angusta*. Chromosome number $2n = 20$.

Flowering time: Late September to November.

Distribution: Mountains and flats, often on clay soil, from Cedarberg in the north to the Bredasdorp district in the south east.—FIG. 25.

The differences between *Moraea anomala* and its close allies *M. neglecta* and *M. angusta* are discussed in detail under the last mentioned species. *Moraea anomala* itself can usually be distinguished by its two bract leaves, smooth nodes, and pale yellow flower with filaments distinctly united for at least 2 mm and between ⅓ and ½ the total filament length.

Though the three species assigned to subgenus *Monocephalae* share the same geographical range, there are indications that each has slightly different habitat preferences. *Moraea anomala* is usually found on a clay substrate, either on flats or often on the upper shale band of the mountain ranges, notably in the Cedarberg and in the Du Toits Kloof Mountains. Most forms of *M. anomala* open in the late morning, and last till about 5:00 P.M. the same day. Strangely, the Cedarberg populations appear only to open at this time of the day and represent a fairly distinct form of this species.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Pakhuis Pass (BB), *Salter 1661* (K).
32.19 (Wuppertal): Top of Cedarberg Pass (AC), *Goldblatt 3252* (MO, NBG, PRE, S). Elands Kloof (CA), *Barker 3121* (NBG); *Lewis s.n.* (BOL-24394).
33.18 (Cape Town): Skeleton buttress, Kirstenbosch (CD), *Compton 16598* (STE).
33.19 (Worcester): Top of Du Toits Kloof Pass (CA), *Goldblatt 3201* (MO). Slopes of Naudesberg, Koo (DA) *Jessop s.n.* (NBG-58973).
34.18 (Simonstown): Hottentots Holland Mountains above Gordons Bay (BB), *Goldblatt 2988* (MO).
34.19 (Caledon): Lebanon Forest Reserve (AA), *Haynes 501* (PRE, STE); *Kruger 230* (PRE). Top of Houw Hoek Pass, *Gillett 875* (STE); *Lewis s.n.* (SAM-58100). Near Caledon (AB), *Schlechter 5528* (BR, PRE). 5 km W of Elim (DA), *Goldblatt 2616* (MO, PRE, NBG).

30. **Moraea neglecta** Lewis, J. S. African Bot. 15: 118. 1949. TYPE: South Africa, Cape, near Sirkels Vlei, Cape Peninsula, *Lewis s.n.* (SAM-57107, holotype).

Plants similar to *M. angusta*, often more robust. *Stem* bearing 1 bract leaf, rarely 2; nodes viscous. *Spathes* 5–7.5 cm long. *Flowers* deep yellow, the nectar guide lined with black dots; outer tepals 3.8–5 cm long, the limb 2–2.5 cm; inner tepals 2.5–3.5 cm long, usually erect, oblong. *Filaments* 6–12 mm long, united only at the base; *anthers* 7–9 mm long, the pollen yellow. *Style branches* 1.4–1.8 (–2.2) cm long, the crests 1.2–1.7(–2.2) cm, usually slightly shorter than the style branches. *Capsule* and *seed* as in *M. angusta*. Chromosome number $2n = 20$.

Flowering time: Mid September to November.

Distribution: Usually on flats, on sandy soils, from Niuewoudtville in the north to the Caledon district in the southwest.—FIG. 25.

Moraea neglecta is readily distinguished from its two close allies, *M. angusta* and *M. anomala*, when living by its distinctive dark yellow flower with a black dotted nectar guide. It can also be recognised by its usually sticky nodes, single bract leaf, and style crests which are usually slightly shorter than the style branches. Frequently the most robust of the three species, it occurs mainly on sandy flats near the coast between Stanford in the south and the Olifants River

mouth, but is also recorded inland in the Cedarberg, and at Nieuwoudtville, its most northerly extention.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): 30 km SSW of Vredendal (CC), *Acocks 19710* (K, M, PRE, SRGH).

32.18 (Clanwilliam): Het Kruis, Piketberg (DA), *Stephens 8602* (K).

32.19 (Wuppertal): Slopes above Algeria, Cedarberg (AC), *Goldblatt 3256* (MO).

33.18 (Cape Town): Bok Point (CB), *Kies 170* (NBG). Near Mamre, *Barker 8151* (NBG). Sandy fields, Kenilworth (CD), *Bolus 3802* (BM, BOL, K, PRE). Flats at Rondebosch, *Wolley Dod 598* (BM, BOL, K). Camps Bay, *Cassidy 33* (NBG). Durbanville (DC), *Compton 16049* (NBG).

33.19 (Worcester): Saron (AA), *Schlechter 10659* (BM, BR, K, PRE, S). Schoongesig, Ceres (AD), *Hankekom 790* (K, PRE).

34.18 (Simonstown): W slopes, Red Hill (AB), *Hafstom & Acocks 324* (PRE). Kommetje, *Barker 5886* (NBG). Kalk Bay, above Boyes Drive, *Goldblatt 3122* (MO, NBG, PRE). Sirkels Vlei, Cape Point Nature Reserve (AD), *Taylor 8223* (STE); *Lewis s.n.* (K, SAM-57107). Olifantsbosch, *Compton 23709* (NBG). Klaasjagers' flats, *Barker 5903* (NBG, PRE).

34.19 (Caledon): Between Stanford and Hermanus (AD), *Goldblatt 2999* (MO, NBG, PRE). E of Stanford (BC), *Goldblatt 3007* (MO). Franche Kraal (CB), *Barker 8499* (NBG).

IV. Subgenus VIEUSSEUXIA

Subgenus **Vieusseuxia** (de la Roche) Baker, Handbook Irid. 48. 1892; Fl. Cap. 6: 12. 1896. TYPE: *Vieusseuxia spiralis* de la Roche = *Moraea bellendenii* (Sweet) N.E. Br.

Vieusseuxia de la Roche, Diss. Pl. Nov. 14. 1766.

Plants medium to small, simple to many branched. *Leaves* 5–1, solitary in most species. *Stem* produced above ground. *Flowers* unmodified to variously specialized with the inner tepals entire, tricuspidate, aristate or lacking. *Style branches* large with well-developed crests or, in a few species, much reduced to ± lacking. *Capsule* clavate to cylindrical; *seeds* small, angular or larger with inflated testa. Basic chromosome number $x = 6$.

Distribution: Southern, central and east Africa as far north as Sudan and Ethiopia.

This, the largest of the 5 subgenera of *Moraea*, comprises about 35 species, ranging in form from the large, many-branched multi-leafed *Moraea polystachya* to such specialized species as *M. villosa* and its allies with their often unbranched stems, single leaf, and gorgeously colored flowers with characteristic tricuspidate inner tepals. The chromosome number is based on $x = 6$ throughout the subgenus, and only a few polyploid species are known.

Subgenus *Vieusseuxia* is believed to have evolved from subgenus *Moraea* or an immediate ancestor (Goldblatt, 1976a) with species like *M. polystachya* and *M. polyanthos*, the most primitive in the subgenus, bridging the gap between the multi-leafed, many-branched ancestral habit and the single leaf and simple or few-branched habit of the majority of species in the subgenus.

Section 6. **Polyanthes** Goldbl., Ann. Missouri Bot. Gard. 63: 8. 1976. TYPE: *Moraea polystachya* (L.f.) Ker.

Plants medium to small, few to many branched. *Leaves* 5–3 or solitary. *Flowers* blue purple; inner tepals entire, spreading or erect. *Style branches* and crests

well developed. *Capsule* spherical-clavate; *seeds* small, angled. Basic chromosome number $x = 6$.

Distribution: Southern Cape, the karoo, South West Africa, through the central and east African highlands to Sudan and Ethiopia.

Section *Polyanthes* is a natural alliance comprising species ranging from the several-leafed, much-branched forms such as *Moraea polystachya* and *M. polyanthos* to fewer-branched species including amongst others, *M. carsonii* Baker with only two leaves, in tropical Africa, and the single leafed *M. elliotii* Baker and *M. stricta* Baker from southern Africa. Though most of the approximately ten species in the section occur in summer rainfall regions of Africa, the putatively more primitive multi-leaved species occur in the south in the karoo and southern Cape.

31. **Moraea polystachya** (L.f.) Ker

This widespread species occurs predominantly in the summer rainfall area and it was treated fully in the revision of *Moraea* for this area (Goldblatt, 1973: 217). It occurs primarily in South Africa in the Great Karoo and eastern Cape and extends not only into South West Africa, Botswana, and the northern Cape, but also into the Little Karoo, an area recognized as part of the winter rainfall region. Field observations have indicated that the populations occurring in the Little Karoo are distinctive and comprise what may be regarded as a geographical race. The populations in the Little Karoo have paler blue flowers than the typical form, erect inner tepals, and lack the characteristic red venation of the ovary found in plants occurring outside this area. The Little Karoo populations are also later blooming, from June to August, while the typical flowering period of plants in the summer rainfall region is April and May occasionally extending to early July.

32. **Moraea polyanthos** L.f., Suppl. Pl. 99. 1781; Baker, Fl. Cap. 6: 16. 1896. TYPE: South Africa, Cape, Kore R. region, *Thunberg s.n.* (Herb. Thunb. 1127, UPS, holotype).—FIG. 26A–B.

M. bipartita L. Bolus, J. Bot. 71: 122. 1933. TYPE: South Africa, Cape, Riversdale Karoo, on road to Adams Kraal, *Ferguson s.n.* (BOL-20068, holotype).

Plants (10–)20–30 cm high, occasionally reaching 40 cm, usually much branched. *Corms* ca. 1.5 cm in diameter; tunics of dark brown to black fibers. *Leaves* usually 3, occasionally 2 or 4, linear, 2–6 mm wide, glabrous, the lower basal and usually exceeding the inflorescence, the upper shorter. *Stem* glabrous, branching repeatedly. *Spathes* herbaceous or becoming dry above, the apex attenuate, dark brown; inner spathe (2)2.5–4.5 cm long, the outer ca. half the length of the inner. *Flowers* pale blue; outer tepals (1.6–)2–3 cm long, lanceolate, the limb reflexed to 45°, ca. equal the claw; inner tepals smaller, 1.4–2.5 cm long, lanceolate, also reflexed. *Filaments* 4–6 mm long, free in the upper 1–2 mm; *anthers* ca. 5 mm long. *Style branches* ca. 5 mm long, the crests 5–8 mm. *Capsule* oblong to broadly ovate, ca. 9 mm long; *seeds* angled. Chromosome number $2n = 12$.

Flowering time: (June to) August to October (to November); flowers opening after midday and fading between 5:30 and 6:00 P.M.

Distribution: Common in the Little Karoo, also occasional in dry situations in the southern Cape as far east as Uitenhage.—FIG. 26.

Moraea polyanthos is closely allied to the widespread karoo and eastern Cape, autumn-flowering species, *M. polystachya*, and the two are easily confused. *Moraea polystachya* is however a more robust species and is larger in most features and consistently so in the floral parts. In contrast to *M. polyanthos* which is spring blooming, usually from August to October, *M. polystachya* flowers in the autumn, typically from March to June, but later, in July and August, in the Little Karoo. Though the two species both grow in the Little Karoo and in similar situations, differences in flowering periods appear to isolate them reproductively, with *M. polyanthos* usually blooming several weeks later than *M. polystachya* in the same localities.

Moraea bipartita appears to be no more than a small depauperate form of *M. polyanthos* and is here reduced to synonymy. Its distinguishing feature, the stigma, which instead of being a continuous lip above the anther is divided into two separate lobes, is not unique or even unusual in *Moraea* and is not taxonomically significant, as many forms of *M. polyanthos* also exhibit this feature. Though *M. bipartita* is described as having only two leaves, one of the two specimens of the type collection actually has three leaves, the number most common in *M. polyanthos*.

Moraea polyanthos was first collected by Thunberg whose manuscript name the younger Linnaeus used when describing the species. Both Thunberg and the younger Linnaeus used the name *Iris* for species of *Moraea*, but for some reason *M. polyanthos* was considered a *Moraea*, a genus in their estimation comprising plants with spreading subequal tepals and slender style branches. Apparently the latter were overlooked or not considered significant in this case, for the type of *M. polyanthos* is certainly a true *Moraea*.

SOUTH AFRICA. CAPE: 32.24 (Graaff Reinet): Near Graaff Reinet (BC), *H. Bolus 522* (BOL, K, S).

33.20 (Montagu): Bonnievale (CC), *Marloth 11821* (PRE). Barrydale (DC), *Bayliss 1674* (PRE).

33.21 (Ladismith): Seven Weeks Poort (AD), *Thorne s.n.* (NBG); *Compton 7475* (BOL, NBG); *Goldblatt 661* (BOL); Hoeko road, Ladismith, *Wurts 1117* (NBG). 9 km E of Amalienstein (BC), *Acocks 15300* (PRE).

33.22 (Oudtshoorn): Doornkraal, de Rust (BC), *Dahlstrand 2171* (PRE). Near Ruitersbos (CC), *Salter 3268* (BOL, K).

33.23 (Willowmore): Willowmore (AD), *Bayliss 3615* (NBG). Baviaanskloof (BC), *Bayliss 3619* (NBG). Uniondale (CA), *Paterson 3089* (GRA). Haarlem (CB), *Schonland 3108* (GRA).

33.24 (Steytlerville): Hankey (DD), *Paterson 1* (GRA); *Fourcade 3313* (BOL, K, NBG).

33.25 (Port Elizabeth): Enon (BC), *Thode A2760* (PRE). Uitenhage (CD), *Loubser 904* (NBG); *Dahlstrand 327* (GRA); *Paterson 1164* (GRA). Addo (DA), *Long 1094* (GRA, K, PRE). Port Elizabeth (DA), *Fries et al. 623* (K, PRE, S); *Drège 289* (GRA).

34.21 (Riversdale): Corente River, Riversdale dist. (AA), *Muir 5352* (PRE). Near Gouritz R. bridge (BA), *Mauve 4601* (PRE).

34.22 (Mossel Bay): Hartenbos R., Mossel Bay (AA), *Immelman 91* (PRE). Near Great Brak R., *Young 5542* (BOL).

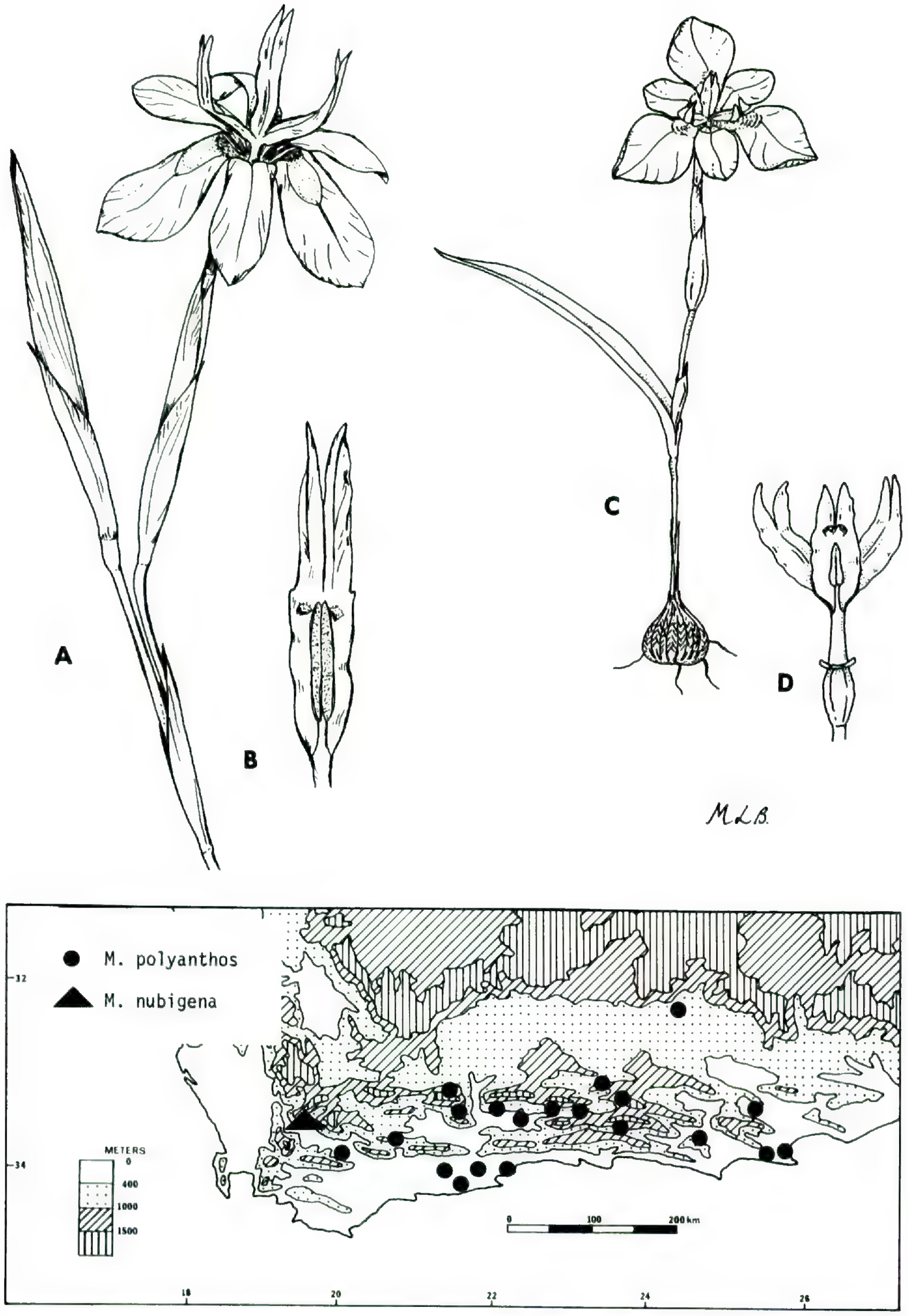


FIGURE 26. Morphology and distribution of *Moraea polyanthos* and *M. nubigena*.—A–B. *M. polyanthos*.—A. Flower (× 1.5).—B. Style branch and anther (× 2).—C–D. *M. nubigena*.—C. Whole plant (× 1.5).—D. Gynoecium and androecium (× 2.5).

33. **Moraea nubigena** Goldbl., sp. nov. TYPE: South Africa, Cape, Worcester district, near Fonteintjiesberg hut at 1,400 m, *Goldblatt 4208* (MO, holotype; K, NBG, PRE, S, isotypes).—FIG. 26C–D.

Planta parva, 3–5 cm alta. *Folium* unum, basale, falcatum, canaliculatum, 3–4 cm longum. *Caulis* simplex. *Spatha* herbacea, interiora 1.2–1.4 cm longa, exteriora breviora. *Flores* 2(–3), atrocaerulei, luteo punctati; tepala exteriora 10–14 mm longa, limbo reflexo; tepala interiora 8–10 mm longa, reflexa. *Filamenta* ca. 3 mm longa, *antherae* 1.5–2 mm longa. *Rami styli* lati, ca. 3 mm longi, cristae ad 2 mm.

Plants very small, 3–5 cm high at flowering time. *Corm* to 1 cm in diameter, spherical, thickly covered with finely reticulate tunics. *Leaf solitary*, inserted at ground level, somewhat succulent, falcate, channelled, 3–4 cm long. *Stem* simple, 2 internodes long with a node and a short bract near the base. *Spathes* herbaceous, often red flushed; inner spathe 1.2–1.4 cm long, the outer ca. ⅔ the inner. *Flowers* 2(–3), deep blue, the nectar guide small, yellow; outer tepals longer than the inner, 1.0–1.4 cm long, the limb 6–8 mm long; flexed sharply 30°–45°, striped; inner tepals 8–10 mm long, the limb also sharply reflexed. *Filaments* ca. 3 mm long, free in the upper third; *anthers* 1.5–2 mm long. *Style branches* 3 mm long, the *crests* to 2 mm. *Capsule* and *seeds* not known. Chromosome number unknown.

Flowering time: Late September.

Distribution: Known only from Fonteintjiesberg in the Worcester district, growing on wet moss-covered rocks at 1,400 m.—FIG. 26.

Moraea nubigena was apparently first gathered in 1925 by the well-known collector of Cape mountain flora, T. P. Stokoe, who gave to Rudolf Marloth two fruiting specimens, now preserved at the National Herbarium in Pretoria. Though not possible to assign to genus, these plants clearly were related to the *Moraea-Homeria* alliance. The locality of the original gathering, the Brandwacht Mountains, was accordingly visited in September 1976, and a population was located on Fonteintjiesberg, adjacent to Brandwacht Mountain, only very locally at about 1,400 m near the mountain club hut.

The species is remarkable in the genus for its size, by far the smallest *Moraea*, and also for its habitat. It grows on moist rock flushes in banks of moss where the very shallow soil inhibits the growth of larger plants. In spite of its specialized habitat and vegetative morphology, the flower itself is quite typical of *Moraea* and not at all modified. It is somewhat tentatively assigned to subgenus *Vieusseuxia* on account of its unbranched habit, and to section *Polyanthes* where its flower is quite typical. Chromosome studies are needed to confirm its affinities.

SOUTH AFRICA. CAPE: 33.19 (Worcester): Brandwacht Mountains (CD), *Stokoe s.n.* (PRE). Fonteintjiesberg, near mountain club hut, on rock flushes, *Goldblatt 4091* (MO), *4208* (K, MO, NBG, PRE, S).

Section 7. **Vieusseuxia**. TYPE: *Vieusseuxia spiralis* de la Roche = *Moraea bellendenii* (Sweet) N.E. Br.

Plants medium to small. Stem simple to several branched. *Leaves* solitary, rarely with a smaller second leaf. *Flowers* variable; inner tepals entire, tricuspidate, aristate or lacking; outer tepals often with conspicuously colored

nectar guides. *Capsules* clavate to cylindrical; *seeds* small, angled, or larger with a spongy testa. Basic chromosome number $x = 6$.

Distribution: Throughout the winter rainfall area and extending north through Natal to the northern Transvaal.

Several natural groups of species can be discerned in this large section of approximately 25 species, but they are closely linked to one another through intermediates, making it difficult to recognize subordinate taxa. The dividing line between section *Vieusseuxia* and section *Polyanthes* is itself rather arbitrary with *Moraea algoensis* and *M. elliotii* being fairly closely related and linking the two sections.

There are three major alliances within section *Vieusseuxia*: *M. tripetala* and its allies form one group; *M. tricuspidata* and *M. unguiculata* and their allies a second; while the so called "peacock moraeas," *M. villosa* and allied species a third. Species like *M. thomasiae* and *M. barkerae*, both with entire inner tepals, are difficult to place and probably represent isolated entities within the section.

Section *Vieusseuxia* contains some of the most advanced species in the genus, and the section as a whole is characterized by a variety of floral specializations, while the vegetative morphology is fairly constant. The center of evolution for the section is probably the southwestern Cape winter rainfall area, but a fair representation of species occurs in the summer rainfall highlands of South Africa.

34. **Moraea algoensis** Goldbl., Ann. Missouri Bot. Gard. 60: 226. 1973. TYPE: South Africa, Cape, Port Elizabeth, *Batten 7* (NBG, holotype).—FIG. 28A.

Plants 20–40 cm high. *Corm* 1–1.5 cm in diameter; coarse tunics often extending upward. *Leaf* linear, inserted near ground level, canaliculate, 2–3 mm wide, exceeding the inflorescence. *Scape* branched, the branches 2–4, held away from the axis, often secund; bract leaves to 4 cm long, dry and brown in the upper part with long, tapering apices. *Spathes* herbaceous with dry apices; inner spathe 4–5 cm long, the outer ca. half the length of the inner. *Flowers* dark blue with yellow nectar guides; outer tepals to 3.0 cm long, the limb ca. 2.0 cm long and ca. 0.9 cm broad; inner tepals blue or brown, comparatively short, 6–10 mm long, reaching to about the level of the stigmas, often distinctly unguiculate with an expanded limb to 2.5 mm broad, entire or occasionally 3-lobed. *Filaments* 3.5–7 mm long, usually free in the upper third; *anthers* 4–7 mm, not reaching the stigmas, pollen orange yellow. *Style branches* 5–8 mm long, the crests linear, up to 8 mm long. *Capsule* clavate, to 1.2 cm long; *seeds* angled. Chromosome number $2n = 12$.

Flowering time: July to September.

Distribution: Southern Cape between Worcester and Port Elizabeth.—FIG. 27.

When first described (Goldblatt, 1973), *Moraea algoensis* was believed to occur mainly in the Port Elizabeth-Humansdorp region, with a westerly extension to the upper Long Kloof near Avontuur. It was consequently regarded as a species from the summer rainfall area of South Africa, Port Elizabeth being a borderline

region. It has subsequently become clear that the Port Elizabeth populations are an easterly extension of a truly winter rainfall area species and it has been collected further west on the Wildehondekloof Pass between Barrydale and Montagu and at the Karoo Garden near Worcester. The Wildehondekloof record *Goldblatt 2840* is of particular interest as *M. tripetala*, a closely related species, was found at the same site. The two species flower at the same time and are superficially similar, but the expanded, though short, inner tepals and well-developed style and united filaments of *M. algoensis* stand in marked contrast to the vestigial inner tepals and almost free filaments and short style, which branches near the base, in *M. tripetala*.

Moraea algoensis appears to represent a link between section *Polyanthes* and section *Vieusseuxia*, with species like *M. elliotii* and *M. carsonii* of the former section being very closely allied to *M. algoensis*, which in turn is related to *M. tripetala*. The inclusion of *M. algoensis* in section *Vieusseuxia* is thus almost arbitrary, though it is placed here because of its small, unusually shaped inner tepals which appear to represent an early step in the reduction of this organ.

SOUTH AFRICA. CAPE: 33.19 (Worcester): Karoo Garden, Worcester (CB), *Olivier 138* (STE).

33.20 (Montagu): Wildehondekloof Pass, W of Barrydale, Little Karoo (DC), *Goldblatt 2840* (K, MO, NBG, PRE).

33.23 (Willowmore): Between Knysna and Avontuur (CC), *Fries et al. 1790* (SAM). Prince Alfred Pass, *Wall s.n.* (S).

33.24 (Steytlerville): Assegaibosch (CD), *Fourcade 1427* (K, BOL). Zuuranys Pass, N. Kareedouw, *Oliver 4438* (STE). 70 km W of Port Elizabeth (DD), *Story 2834* (PRE).

33.25 (Port Elizabeth): Van Stadens Mts. (CC), *Oliver 4472* (STE). Witteklip flats, *Holland s.n.* (BOL-30812); *Long 652* (PRE). Port Elizabeth (DC), *Hafstrom & Acocks s.n.* (PRE-31513). Redhouse, *Paterson 439* (BOL). Near Port Elizabeth, *West 311* (BOL); *Batten 7* (NBG).

34.24 (Humansdorp): Humansdorp (BB), *Loubser 880* (NBG); *Galpin 4646* (K, PRE).

35. **Moraea tripetala** (L.f.) Ker, Bot. Mag. *tab. 702.* 1802; Baker, Fl. Cap. 6: 23. 1896, incl. var.—FIG. 28B.

Iris tripetala L.f., Suppl. Pl. 97. 1786. TYPE: South Africa, Cape, hills near Cape Town, near Piketberg, etc., *Thunberg s.n.* (Herb. Thunb. 1186, UPS, lectotype).

Vieusseuxia tripetala (L.f.) Klatt, Durand & Schinz, Consp. Fl. Afr. 5: 155. 1895.

Moraea tripetala var. *jacquinii* Schlecht. ex Lewis, J. S. African Bot. 7: 54. 1941. TYPE: South Africa, Cape, Constantiaberg, *Wolley Dod 1919* (BOL, lectotype).

Vieusseuxia tripetaloides DC., Ann. Mus. Natl. Hist. Nat. 2: 138. 1803, nom. illeg., superfl. pro *Iris tripetala* L.f.

Iris mutila Licht. ex R. & S., Syst. Veg. 1: 477. 1817. TYPE: South Africa, Cape, Lions Head, *Lichtenstein s.n.* (Location of specimen unknown).

Moraea tripetala var. *mutila* (Licht. ex R. & S.) Baker, Fl. Cap. 6: 23. 1896.

Vieusseuxia pulchra Eckl., Top. Verz. 13. 1827. TYPE: South Africa, Cape, "Hottentotskloof," *Ecklon & Zeyher s.n.* (S, lectotype).

V. mutila C. H. Berg ex Eckl., Top. Verz. 12. 1827. TYPE: South Africa, Cape, Camps Bay *Berg s.n.* (S, lectotype).

Moraea punctata Baker, Bull. Herb. Boissier, sér. 2, 4: 1003. 1904. TYPE: South Africa, Cape, Gouda (as Piketberg Road), *Schlechter 4851* (K, lectotype; B, PRE, isotypes).

M. monophylla Baker, Bull. Misc. Inform. 1906: 24. 1906. TYPE: South Africa, Cape, Olifants Rivier, *Penther 685* (K, lectotype), *626* (K, syntype).

M. amabilis Diels, Bot. Jahrb. Syst. 44: 118. 1910. TYPE: South Africa, Cape, "Bokkeveld, Oorlogs Kloof," Calvinia, *Diels 626* (B, lectotype).

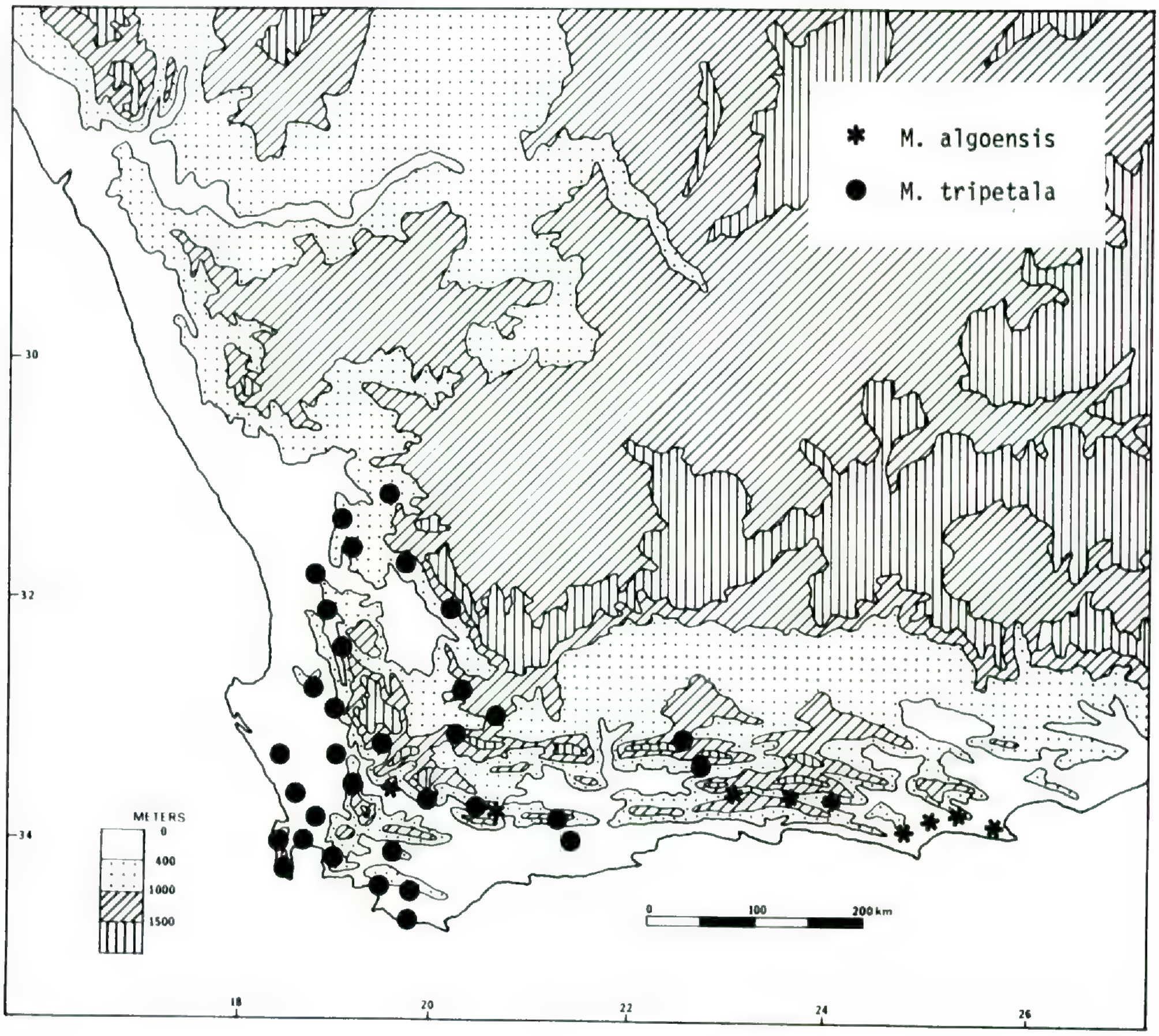


FIGURE 27. Distribution of *Moraea algoensis* and *M. tripetala*.

Plants 10–50 cm high, simple or few branched. *Corm* 1–2 cm in diameter; tunics pale to dark grey, fine to coarsely fibrous. *Leaf* solitary or rarely 2, basal, canaliculate, linear or ensiform, glabrous or pubescent. *Stem* simple or with divergent branches. *Spathes* herbaceous, with dark brown attenuate apices; inner spathe 3.5–7 cm long, the outer ca. half the inner. *Flower* pale to dark blue, or pale pink, the nectar guide white to yellow; outer tepals lanceolate, 2–3.5 cm long, the claw to 1.5 cm long, bearded and often spotted, the limb spreading to somewhat reflexed; inner tepals inconspicuous, rarely tricuspidate with a longer central cusp, usually filiform or ciliate, occasionally absent. *Filaments* 4–6 mm long, joined at the base only; *anthers* 4–8 mm long, the pollen usually red. *Style branches* 7–10 mm long, the crests 5–15 cm long, linear-lanceolate. *Capsule* clavate, 1.3–1.6 cm long; *seeds* small, angular. Chromosome number $2n = 12$.

Flowering time: August to December, latest at high altitudes.

Distribution: Southwestern Cape from Nieuwoudtville in the north to Riversdale in the east, occurring both on clay and sandy soils.—FIG. 27.

The extremely variable *Moraea tripetala* is treated here as a single aggregate species and no subspecific taxa are recognized. All forms share in common the

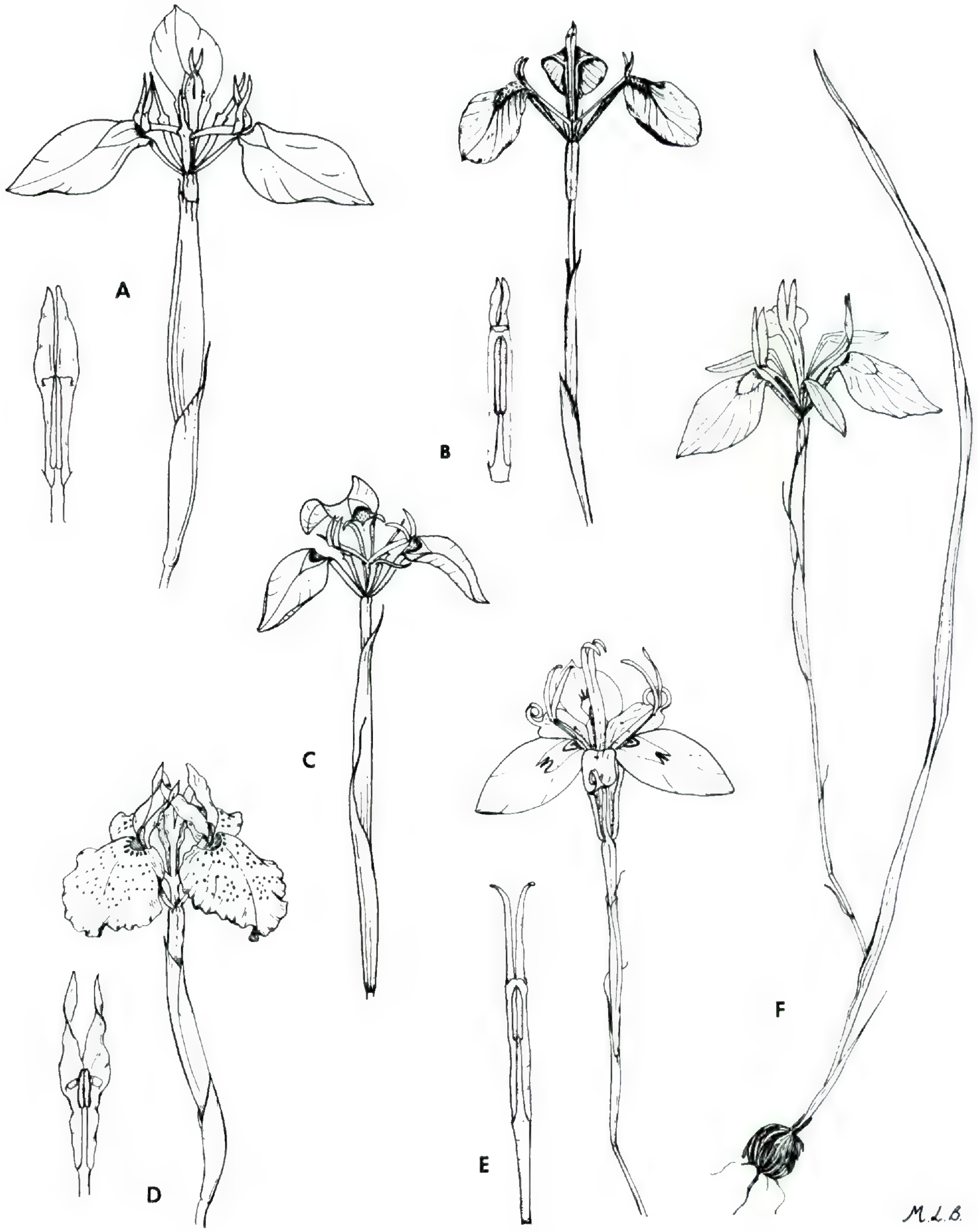


FIGURE 28. Morphology of *Moraea* species.—A. *M. algoensis*.—B. *M. tripetala*.—C. *M. debilis*.—D. *M. barnardii*.—E. *M. barkerae*.—F. *M. thomasiae*. (Flowers life size, stamens and style branches ca. ×2.)

almost free filaments that are barely united at the base, a feature otherwise found only in the related *M. barnardii*. The latter is distinguished by its white flower which lacks inner tepals entirely.

All forms of *M. tripetala* are slender and often have an unbranched stem; there is, however, considerable variation in flower size, form, and particularly in

the structure of the inner tepals. The latter are most often short and spikelike but are occasionally trifid or may be entirely absent. The color and texture of the corm tunics is also notably variable. This character is evidently linked to the wide range of soils on which the species grows. Plants from sandy areas with adequate moisture tend to have small corms with dark tunics, while plants in drier sandy soils have larger corms with very coarse dark fibers. In general, plants on clay soils in dry areas have large corms with very pale tunics which have fine inner fibers but quite coarse outer layers. This rule does not hold in all cases as small dark corms may be encountered among plants on a clay substrate.

The species is common throughout the entire southwestern Cape from Nieuwoudtville in the north to Mossel Bay. It is particularly tolerant of arid conditions and extends further inland than most winter rainfall species of *Moraea*, to Calvinia, Sutherland and Prince Albert.

The following major forms can be distinguished:

a. A robust large-flowered form occurring on sandy soils in the Caledon and Cape Town districts.

b. A tall, branched, very pale blue form from the Clanwilliam, Calvinia and Van Rhynsdorp areas (*M. amabilis*).

c. Short, small, purple-flowered plants found on clay slopes in the Ceres district.

d. A very short form with purple flowers and a single, or often 2 very narrow leaves, from arid areas of the Little Karoo, Matjesfontein and Touws River districts.

e. Early flowering, quite large-flowered plants with a pubescent leaf, in the Cape Town–Malmesbury area (*Iris mutila*).

f. A very late flowering (November–January), small-flowered form from higher altitudes in the southwestern Cape, usually on sandy soils (*M. tripetala* var. *jacquinii*).

The morphological variability of *M. tripetala* is mirrored in a degree of karyotypic variation unusual in *Moraea*. Though all forms so far examined have a diploid number of $2n = 12$, variation in proportions of chromosome arms and in satellite location indicate considerable cytological differentiation of various races. When sufficient material has been studied it will hopefully become possible to correlate cytological and morphological variation to form a coherent picture of evolution in the species.

SOUTH AFRICA. CAPE: 31.18 (Van Rhynsdorp): Top of Giftberg Pass (DB), *Thompson 484* (STE). Bullshoek (DD), *Schlechter* 8383 (K, MO, PRE, S).

31.19 (Calvinia): W of Nieuwoudtville (AC), *Lewis s.n.* (SAM-60842); *Marloth 7640* (PRE). Glenlyon, Nieuwoudtville, *Hardy 73* (PRE); *Goldblatt 3098* (MO). Lokenberg, *Acocks 18900* (K, PRE). 10 km SW of Calvinia (DA), *Acocks 19491* (M, PRE, S).

32.18 (Clanwilliam): Olifants River at Clanwilliam, (BB), *Penther 685* (K). Boskloof road, near Clanwilliam, *Goldblatt 2457* (K, MO, NBG, PRE, S). Piketberg Mt. (DC), *Stokoe s.n.* (SAM-55635); *Barker 7563* (NBG). Flats near Porterville (DD), *Loubser 937* (NBG).

32.20 (Sutherland): Koedoes Mts. (CD), *Goldblatt 547* (BOL). 70 km S of Sutherland (DC), *Goldblatt 3222* (MO).

33.18 (Cape Town): Ysterfontein (AC), *Lewis Grant 2580* (MO). Bokbaai (BB), *van der Merwe 1594* (PRE). Lions Head, Cape Peninsula (CD), *Prior s.n.* (K, PRE). Kenilworth, *H. Bolus 5692* (BOL, PRE). Table Mt., *Marloth 7280, 6051* (both PRE). Between the Salt

River and Kalabas Kraal (DA), *Hutchinson 161a* (K, PRE). Stellenbosch (DD), *Strey 559, 560* (PRE).

33.19 (Worcester): Lower slopes, Gydo Pass (AB), *Hafstrom & Acocks 323* (PRE). Gydo Pass, *Marloth 10602* (PRE); *Barker 6836* (NBG); Gouda (as Piketberg road) (AC), *Schlechter 4851* (B, GRA, K, PRE). Bainskloof (CA), *Lewis Grant 2235* (MO). Mts. S of Wemmershoek (CC), *Andreae 675* (PRE). Foot of French Hoek Pass, E side (CD), *Marsh 666* (PRE, STE). Lower slopes of Rabiesberg (DA), *Lewis s.n.* (BOL-21733, PRE); *van der Gaast s.n.* (NBG). Foot of Naudesberg, Koo (DB), *Lewis 6054* (NBG).

33.20 (Montagu): Tweedside (AB), *Barker 7466* (NBG). Klein Roggeveld (BA), *Marloth 9595, 9602* (both PRE). Wildehondekloof Pass (DC), *Goldblatt 2839* (MO, NBG, PRE, S).

33.21 (Ladismith): Garcias Pass (CC), *Galpin 4651* (K).

33.22 (Oudtshoorn): Near Cango Caves (AC), *Gillett 1695* (STE). Between Prince Albert and Klaarstroom (A) *Leipoldt s.n.* (PRE).

34.18 (Simonstown): Fish Hoek (AB), *Wedermann & Oberdieck 792* (PRE). Red Hill, Simonstown, *Taylor 5240* (PRE, STE). Sir Lowrys Pass (BB), *Schlechter 7222* (GRA); *Goldblatt 2506* (MO, NBG, S). Hottentots Holland kloof, *Ecklon & Zeyher s.n.* (S). S of Pringle Peak (BD), *Boucher 624* (PRE, STE). Palmiet River mouth, *Gillett 4250* (BR, MO).

34.19 (Caledon): Near Caledon (AB), *H. Bolus 9169, 7878* (both K, PRE). Zwartberg, Caledon, *Schlechter 5556* (BOL, BR, PRE); *Goldblatt 2509* (MO). Kleinrivier Mts., (AD), *Zeyher 1650* (GRA, K). Genadendal (BA) *Lindeberg s.n.* (S). Hills above Pearly Beach (DA), *Goldblatt 2607* (MO).

34.20 (Bredasdorp): Bontebok Park, Swellendam (AB), *Liebenberg 6544* (PRE). De Hoop (AD), *van der Merwe 1077* (PRE). 14 km E of Swellendam (BA), *Marsh 1004* (PRE, STE).

34.21 (Riversdale): Gouritz River bridge (BA), *Galpin 4647* (PRE).

34.22 (Mossel Bay): Goukamma Nature Reserve (BB), *Heineken 206* (PRE).

36. **Moraea debilis** Goldbl., Ann. Missouri Bot. Gard. 63: 21. 1976. TYPE: South Africa, Cape, clay slopes SW of Caledon, *Goldblatt 673* (BOL, holotype; K, MO, PRE, S, isotypes).—FIG. 28C.

Plants slender, 15–40 cm high, usually branched. *Corm* ca. 1 cm in diameter; tunics pale, finely fibrous. *Leaf* solitary, basal, linear, pubescent on the outer surface and/or ciliate on the margins, exceeding the inflorescence. *Stem* laxly branched, rarely simple, the bract leaves dry. *Spathes* herbaceous, or dry above, the apices attenuate or lacerated; inner spathe 4–5.5 cm long, the outer ca. half the inner. *Flowers* purple, fading to a pale mauve and becoming lightly speckled; outer tepals spreading, ca. 2 cm long with a slender bearded claw and a lanceolate limb ca. 1 cm long; inner tepals ca. 1 cm long, erect, filiform, usually tricuspidate with the central cusp much exceeding the laterals. *Filaments* ca. 4 mm long, joined for ca. half the length; *anthers* ca. 5 mm long. *Style branches* ca. 7 mm long, the crests lanceolate, to 3 mm long. *Capsule* narrowly ovoid-clavate; *seeds* angled. Chromosome number $2n = 12$.

Flowering time: September to October.

Distribution: Clay soils in the Caledon district, southwestern Cape.—FIG. 29.

This slender, dainty plant with its small mauve flowers and reduced inner tepals is clearly allied to the well-known and widespread *Moraea tripetala*. *Moraea debilis* grows in clay soils among low growing shrubs in the Caledon district and is typically late flowering. It is distinguished from the related *M. tripetala* and *M. barkerae* by its pubescent leaf and small flowers, which have thread-like, trifid-tricuspidate inner tepals, and by its filaments which are united for about half their length unlike those of its two close allies.

SOUTH AFRICA. CAPE: 34.19 (Caledon): SW of Caledon (AC), *Barnard s.n.* (BOL-30694); *Goldblatt 673* (BOL, K, MO, PRE, S). Between Bot River and Caledon, *Mauve 4893* (PRE). Ca. 12 km E of Caledon (BA), *Barker 10851* (NBG, S).

Without precise locality: Caledon district, *Pappe s.n.* (SAM-70709); *Leipoldt 3562* (BOL); *Schlechter 5527* (BOL, PRE).

37. **Moraea barnardii** L. Bol., J. Bot. 71: 22. 1933. TYPE: South Africa, Cape, top of Shaws Pass, *Barnard s.n.* (BOL-20067, holotype).—FIG. 28D.

Plants small, slender, rarely exceeding 30 cm in height. *Corm* ca. 1 cm in diameter; tunics light brown, coarsely fibrous. *Produced leaf* solitary, linear, canaliculate, usually exceeding the inflorescence, ca. 1.5 mm wide, glabrous. *Stem* terete, simple or 1-branched, bearing 2 bract leaves. *Spathes* dry, brown, acuminate; inner spathe ca. 4.5 cm long, the outer to 2.5 cm long. *Flower* white, marked with blue purple veins and nectar guide; outer tepals ca. 2 cm long, the limb to 1.3 mm long, the margins undulate; inner tepals absent. *Filaments* 8–9 mm long, united at the base for 2 mm; *anthers* oblong, 3–4 mm long, red. *Style branches* ca. 6 mm long, the crests 6–7 mm long, lanceolate. *Capsule* clavate, red flushed, ca. 1 cm long; *seeds* angled. Chromosome number $2n = 12$.

Flowering time: Mid September and early October.

Distribution: Local in the mountains of the Caledon district in sandy soil.—FIG. 29.

This diminutive species is extremely rare, being well known from one locality only, the top of Shaws Pass, between Caledon and Hermanus, where it blooms regularly at the end of September. One collection, however, from Gansbaai, well to the south, suggests that *M. barnardii* may not be as rare as the record indicates.

Moraea barnardii is allied to the widespread *M. tripetala* but differs in having a white flower, delicately veined in purple, undulate outer tepals, and it completely lacks inner tepals. *Moraea tripetala* in contrast is colored blue to purple, or rarely pink, the margins of the outer tepals are straight-edged and rarely are the inner tepals absent—more often they are reduced to short cusps.

SOUTH AFRICA. CAPE: 34.19 (Caledon): Top of Shaws Pass (AD), *Barker 18* (BOL, K); *Barnard s.n.* (BOL-20067, NBG-93752, SAM-69609); *Loubser 2153* (NBG); *Mauve & Barnard 4765* (PRE). Gansbaai (CB), *Gillett 4311* (BOL).

38. **Moraea incurva** Lewis, S. African Gard. 23: 167. 1933. TYPE: South Africa, Cape, between Wellington and Tulbagh, *Stanford s.n.* (BOL-20185, holotype).

Plants slender, 35–40 cm high, unbranched. *Corm* ca. 1.5 cm in diameter; tunics of dark brown fibers. *Leaf* solitary, basal, linear, 2–4 mm wide, exceeding the inflorescence. *Stem* simple, 3–4 internodes long. *Spathes* herbaceous, dry above, attenuate; inner spathe 4–5 cm long, the outer about 2.5 cm long. *Flower* violet blue, the nectar guide yellow; outer tepals ca. 2 cm long, lanceolate, the limb ca. 1.5 cm; inner tepals entire, erect, ca. 1.8 cm long, and to 6 mm wide, the limb curved inward. *Filaments* 1.1 mm long, free near the apex; *anthers* ca. 3 mm long. *Style branches* 4 mm long, the crests ca. 4 mm long. *Capsule* clavate, ca. 1.5 cm long; *seeds* angled. Chromosome number not known.

Flowering time: October.

Distribution: At the foot of the Elandskloof Mountains, probably in clay soil.—Fig. 29.

Moraea incurva is known only from the type specimens, collected somewhere north of Wellington at the foot of the Elandskloof Mountains. It may well be extinct since this area is now intensively farmed. The species appears most closely related to *M. tripetala* from which it differs by its large, entire inner tepals and united filaments. The obvious relationship to *M. tripetala*, and to a lesser extent to *M. unguiculata*, places *M. incurva* almost without doubt in section *Vieusseuxia*, even though it has entire inner tepals. Although unusual in the section, entire inner tepals also occur in *M. insolens*, *M. barkerae*, *M. thomasiae*, as well as in forms of *M. neopavonia* and *M. lurida*.

South Africa. cape: 33.19 (Worcester): Between Wellington and Tulbagh, *Stanford s.n.* (BOL-20185).

39. **Moraea barkerae** Goldbl., sp. nov. type: South Africa, Cape, Cedarberg, 1,400 m, above Algeria on trail to Middelberg, *Goldblatt 3245* (MO, holotype; K, NBG, PRE, S, isotypes).—Fig. 28E.

Planta 30–50 cm alta, simplex vel pauciramosa. *Cormus* ca. 1.5 cm diameter. *Folium* solitarium, lineare, canaliculatum. *Spathae* herbaceae, apice sicco, attenuato. *Flos* pallidum salmoneum, pupureis notatis; tepala exteriora lanceolata, ca. 3 cm longa, limbis effusis; interiora erecta, limbis arcuatis, apicibus attenuatis, integribus vel tricuspidatis. *Filamenta* 1 cm longa, connata in parte dimidia.

Plants 15–40 cm high, occasionally branched. *Corm* to 1.5 cm in diameter; tunics of coarse light brown fibers. *Leaf* solitary, basal, linear, glabrous, much exceeding the inflorescence. *Stem* glabrous, usually simple or bearing 1 branch. *Spathes* herbaceous with dry, dark brown, attenuate apices; inner spathe 5.5–7 cm long, the outer 3–4.5 cm long. *Flowers* white to salmon, with purple markings; outer tepals ca. 3 cm long, lanceolate, the claw to 1 cm, lightly bearded, the limb spreading, ca. 1 cm wide; inner tepals ca. 2.5 cm long, erect, to 6 mm at the widest point, the apex produced as a long slender cusp, usually entire, occasionally trilobed. *Filaments* to 1.5 cm long, united for ca. ⅔ of their length; *anthers* 5 mm long, apiculate. *Style branches* ca. 1 cm long, the crests ensiform, to 1 cm long. *Capsule* and *seeds* not known. Chromosome number $2n = 12$ (*Goldblatt 3245*, type collection).

Flowering time: Late September to November.

Distribution: Mid and upper altitudes in the Cedarberg and Cold Bokkeveld Mountains.—Fig. 29.

Although *Moraea barkerae* has been known for some time, first having been collected by M. A. Pocock in the 1930s, it has remained until now undescribed. It is certainly one of the most beautiful of all moraeas with slender stems bearing delicate salmon to shell pink flowers marked with purple nectar guides. The species is not common, though has been recorded from several different places in the Cedarberg and Cold Bokkeveld Mountains. It occurs from fairly low altitudes such as Elands Kloof, where it flowers in late September, to the high Cedarberg, where flowering is delayed until December.

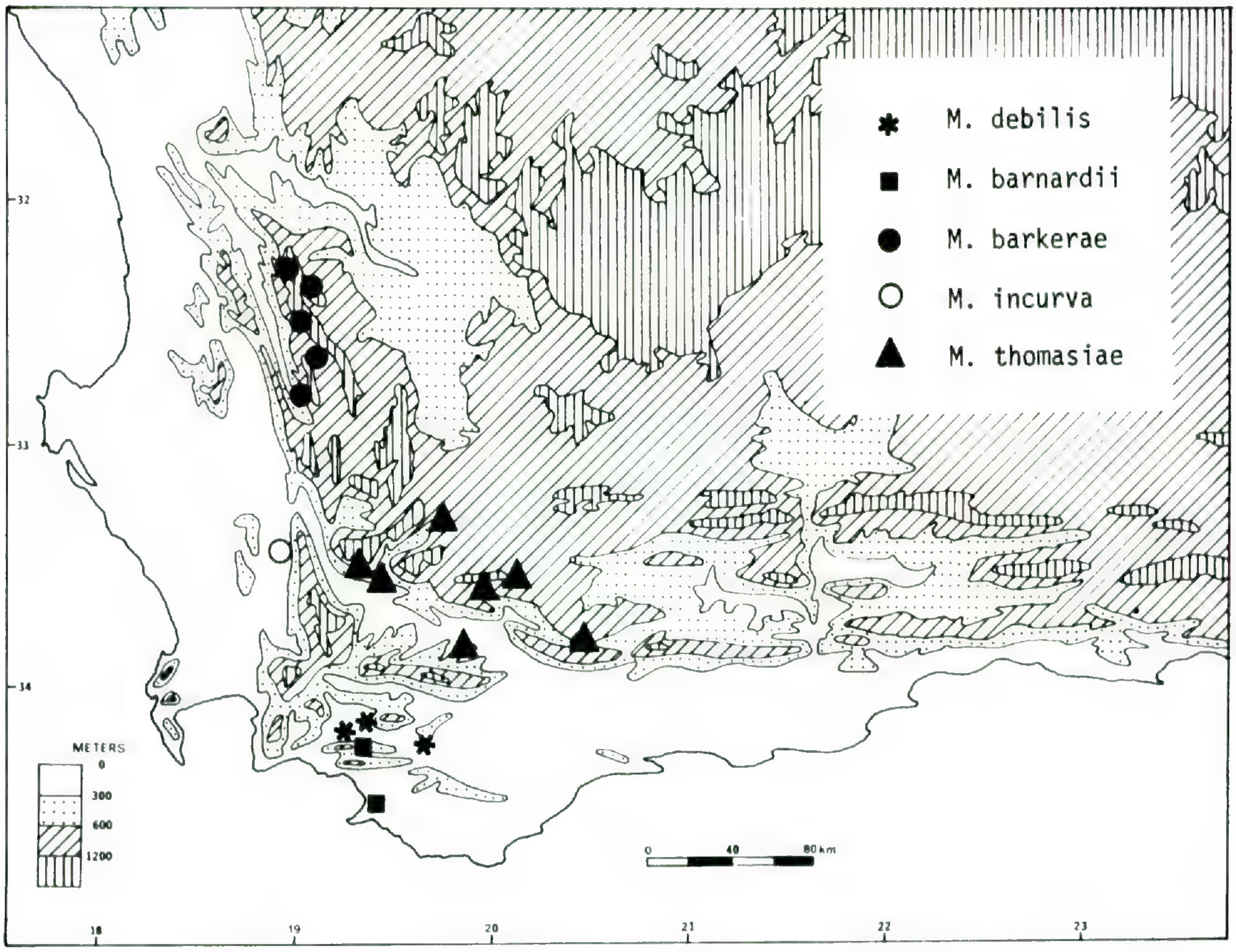


FIGURE 29. Distribution of *Moraea debilis*, *M. barnardii*, *M. barkerae*, *M. incurva*, and *M. thomasiae*.

The inner tepals are usually entire with an erect attenuate incurved limb like that found in *Moraea incurva*. Occasionally, however, the inner tepal is clearly 3-lobed with two small obtuse lateral projections formed at the base of the central attenuate cusp. The slender form and lack of branching suggest affinities with *M. tripetala* and *M. unguiculata* as well as to *M. incurva*, but the relationship is probably not close; *M. barkerae* thus appears rather isolated in section *Vieusseuxia*.

The species is named in honor of Miss F. W. Barker, the well-known South African botanist and retired Curator of the Compton Herbarium, Kirstenbosch. She has long been interested in the bulbous flora of the southwestern Cape, and made one of the first collections of the species now named after her.

SOUTH AFRICA. CAPE: 32.19 (Wuppertal): Near Middelberg, 1400 m, Cedarberg (AC). *Jackson s.n.* (NBG, SAM-68452); *Goldblatt 3245* (MO, NBG, PRE, S), *3260* (MO). Elands Kloof, 1400 m, (CA), *Barker 3103* (NBG, PRE, S). Hoog Verloren, Sneeuberg, Cedarberg, *Pocock 403* (STE). Grootfontein farm, Olifants R. valley, ridge E of farm (CC) *Oliver 3980* (STE).

40. **Moraea thomasiae** Goldbl., Ann. Missouri Bot. Gard. 63: 20. 1976. TYPE: South Africa, Cape, Karoo Garden, Worcester, *Goldblatt 2422* (NBG, holotype; BOL, K, MO, PRE, S, isotypes).—FIG. 28F.

Plants small, slender, 15–30 cm high. *Corm* ca. 1 cm in diameter; tunics dark brown to black. *Leaf* solitary, ± basal, linear, ca. 3 mm wide, glabrous, exceeding the inflorescence. *Stem* simple. *Spathes* herbaceous with brown attenuate apices; inner spathe up to 6 cm long, the outer ca. half the length of the inner. *Flowers* yellow; outer tepals with a narrow, long, erect claw, 1.5 cm long, the limb reflexed, ca. 2 cm long; inner tepals erect, narrowly lanceolate, up to 2 cm long. *Filaments* to 5 mm long, free almost to the base; *anthers* ca. 6 mm long. *Style branches* ca. 1.5 cm long, bearing linear crests ca. 1 cm long. *Capsules* and *seeds* not known. Chromosome number $2n = 12$.

Flowering time: August to mid September.

Distribution: Clay and shale slopes, usually on a south aspect, in the Montagu and Worcester districts.—Fig. 29.

Moraea thomasiae, only recently described, indicates that the southwestern Cape is not as well known botanically as might be expected for an area studied since the 1770s. No specimen is known to have been collected prior to 1945, and yet recently several people have independently found this species in widely separate areas. It is now clear that *M. thomasiae* is common in the Worcester–Montagu area, occurring in semikaroid vegetation where it favors the moister, south-facing slopes of shale hills and banks.

Though very like *M. angusta* in general appearance, *M. thomasiae* is unrelated, and the two belong to different subgenera. *Moraea thomasiae* stands in a rather isolated position in subgenus *Vieusseuxia*; its slender habit, unbranched stem, and solitary leaf suggest no close allies. It can always be distinguished from the similar but unrelated *M. angusta* by its canaliculate leaf, terete ovary, and acuminate spathes, while its yellow flower and long, narrow inner tepal set it apart from certain forms of *M. tripetala* which have similar, almost free filaments.

South Africa. cape: 33.19 (Worcester): Hex Pass, near summit (BD), *Mauve & Oliver 192* (STE). Karoo Garden, Worcester (CD), *Bayer 7* (NBG); *Goldblatt 2422* (K, MO, NBG, PRE, S). Onse Rug Farm, Worcester district, *Barker 9446* (NBG).

33.20 (Montagu): Oudeberg, Montagu district (CA), *Acocks 20539* (NBG, PRE). Burgers Pass, Koo district (BD), *Thomas s.n.* (BOL); *Mauve & Oliver 197* (STE). Vrolikheid, McGregor district (DD), *Jooste 154, 181* (both STE).

41. **Moraea unguiculata** Ker,[7] Bot. Mag. *tab.* 593. 1802. type: Illustration in Bot. Mag. *tab.* 593.—Fig. 30.

Iris tricuspis Thunb. var. *minor* Jacq., Ic. Pl. Rar. 2, *tab. 222.* 1792. type: Illustration in Jacq., Ic. Rar. *tab. 222.* 1792.

Moraea tenuis Ker, Bot. Mag. *tab. 1047.* 1807. type: Illustration in Bot. Mag. *tab. 1047.*

Vieusseuxia tenuis (Ker) R. & S., Syst. Veg. 1: 491. 1817.

Moraea violacea L. Bol., S. African Gard. 28: 116. 1928, nom. illeg., non *M. violacea* Baker.
type: South Africa, Cape, Ceres, *Cook s.n.* (BOL-17020).

M. ceresiana Lewis, J. S. African Bot. 7: 57. 1941, nom. nov. pro *M. violacea* L. Bol.

Plants 15–60 cm high, simple, or few branched. *Corm* 1–2 cm in diameter; tunics pale to dark grey, fine to coarsely fibrous. *Leaf* solitary, basal, linear,

[7] Not to be confused with *Moraea unguicularis* Lam. = *Tritoniopsis unguicularis* (Lam.) Lewis.

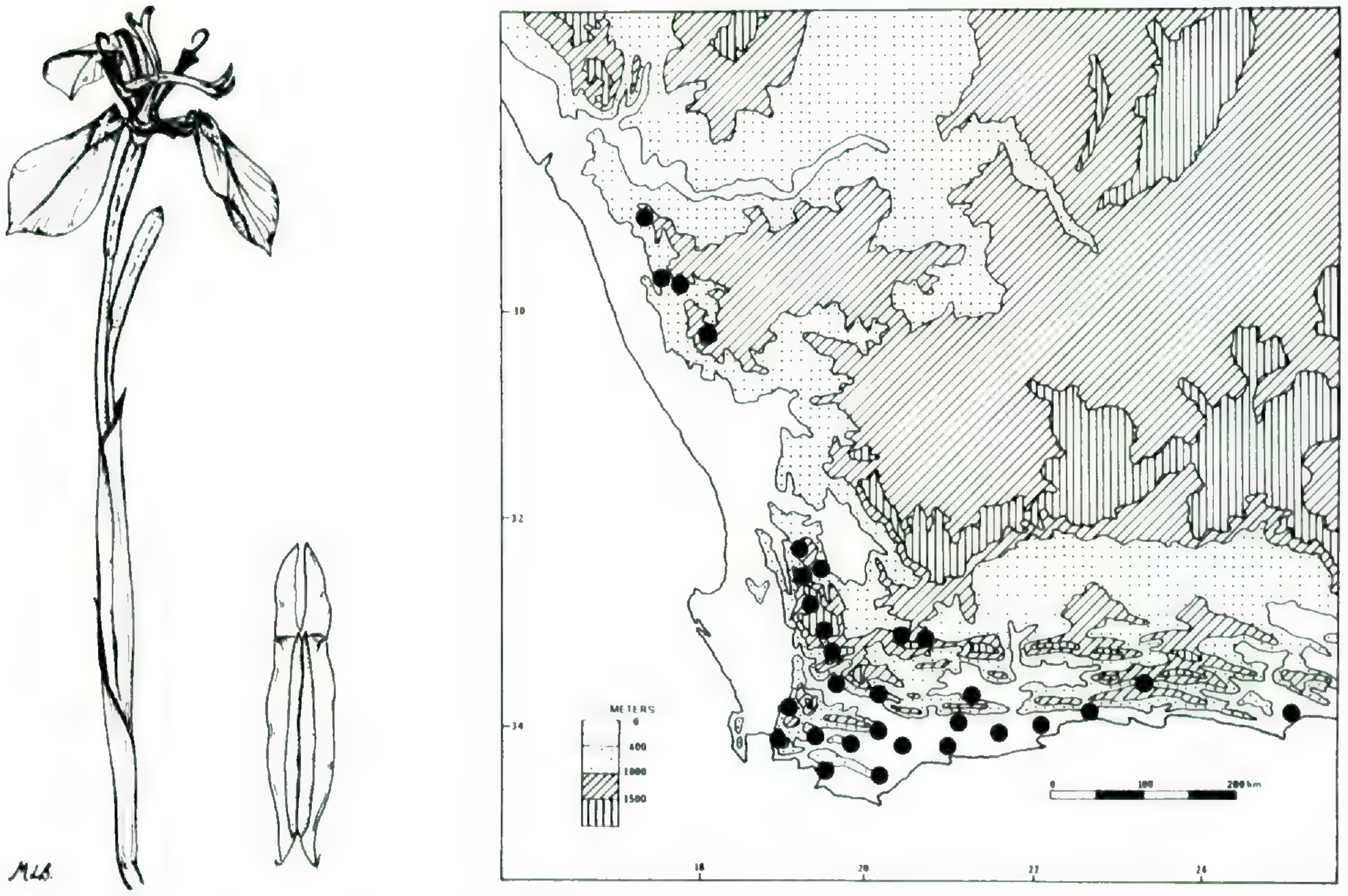


FIGURE 30. Morphology and distribution of *Moraea unguiculata* (life size) with stamen and style branch enlarged.

canaliculate, glabrous. *Stem* simple or more often branched. *Spathes* herbaceous, becoming dry above, the apices attenuate, dark brown; inner spathes 3–5 cm long, the outer ca. half the length of the inner. *Flower* white, cream, yellow, brown or deep blue, the nectar guide yellow; outer tepals lanceolate, 1.2–2.2 cm long, the claw ca. half the length of the limb, bearded, the limb reflexed from 45° to 90°; inner tepals erect, 7–12 mm long, tricuspidate with a long, central, incurved cusp and 2 short obtuse lateral lobes. *Filaments* 4–6 mm long, joined almost to the apex; *anthers* 3–4 mm long, apiculate. *Style branches* ca. 5 mm long, the crests 2.5–4 mm long. *Capsule* clavate, 1.3–1.5 cm long; *seeds* small, angular. Chromosome number $2n = 12$.

Flowering time: October to early December.

Distribution: Widespread throughout the winter rainfall region from Namaqualand in the north to the Humansdorp district in the east and local in the Karoo. —FIG. 30.

Moraea unguiculata has for some time been known by its later synonym, *M. tenuis*. Both species were described by Ker and are typified by plates in Curtis's *Botanical Magazine*. *Moraea tenuis*, described in 1807, is readily identified with the brown-flowered form of *M. unguiculata*. The typical form, dating from 1802, is more difficult to identify as it cannot be matched exactly with any known form of the species. The illustration depicts a white flower, speckled with blue, but while the coloring is unusual, the entirely united filaments and characteristic trifid inner tepals with long and coiled central cusps are distinctive enough to make it almost certain that the type illustration represents a plant conspecific with Ker's later species, *M. tenuis*.

The species is very widely distributed over almost the entire winter rainfall area. It occurs locally on clay soils near Steinkopf and Spektakelberg in Namaqualand, and almost continuously from the Cedarberg, well to the south to the Humansdorp district, though absent from the Cape Peninsula. The small flowers vary in color from white or deep blue to shades of brown, and the latter forms are very inconspicuous. Like *M. tripetala*, the corm tunics appear to vary depending on the soil type; dark, coarse tunics are encountered on sandy soils, while plants on clay have pale tunics with rather finer fibers.

Moraea unguiculata may sometimes be confused with the small forms of *M. tripetala*, especially those with trifid inner tepals, but the united filaments of *M. unguiculata* contrast strongly with the almost free filaments of *M. tripetala*. The two closely related species, *M. bellendenii* and *M. tricuspidata* can be distinguished from *M. unguiculata* by size alone, and also by the inner tepals which in these two species have a short obliquely twisted central cusp, while *M. unguiculata* has a very long, slender and coiled cusp.

South Africa. cape: 29.17 (Springbok): 4.8 km W of Steinkopf (BA), *Goldblatt 2777* (MO); *Acocks 19537* (K, PRE). Modderfontein (BC), *H. Bolus s.n.* (BOL-6618, K). 22 km W of Springbok, foot of Spektakelberg (DA), *Goldblatt 2791* (MO); *Acocks 19574* (K, M, PRE).

30.18 (Kamiesberg): Between Pedroskloof and Leliefontein (D), *Drège 2607, 2609* (both S).

31.24 (Hanover): Leopards Vlei, Richmond district (B), *H. Bolus 14001* (BOL).

32.19 (Wuppertal): Tafelberg, Cedarberg (AC), *Van Niekerk 18169* (BOL). Hoog Verloren, Sneeuberg, *Pocock* 385 (STE). Middelberg plateau, *Compton 12701* (NBG). Krom River Kloof (CA), *Esterhuysen 17975* (BOL, PRE). Gideonskop (CB), *Stokoe s.n.* (SAM-54515). De Keur (CD), *Compton 18793* (NBG).

33.18 (Cape Town): Stellenbosch (DD), *Duthie 285* (BOL). Bankhoek, *Bond* 828 (NBG).

33.19 (Worcester): Gydo Pass (AB), *Bond 715* (NBG). Ceres (AC), *Cook s.n.* (BOL-17020). Prince Alfreds Hamlet, *Oliver 5065* (MO, STE). Schurfdeberg (AD), *Zeyher 4084* (SAM). Lakenvlei, *Olivier s.n.* (NBG-58981). Baviaansberg, NW of Ceres (BA), *Compton 12869* (NBG). San Sebastians Kloof (CA), *Lewis 1614* (SAM). Bains Kloof, *Barker 4646* (NBG). Karoo Garden, Worcester (CB), *Olivier 163* (PRE, STE). Robertson karoo (DD), *Compton 5678* (NBG).

33.20 (Montagu): Whitehill Ridge, S slopes (BA), *Compton 3612* (BOL, NBG), *15174* (NBG). Witteberg, above Elandsfontein, *Nordenstam 3254* (S). Pasture below 10 O'Clock Peak (CD), *Wurts 364* (NBG).

33.21 (Ladismith): Muiskraal (CC), *Galpin 4648* (PRE). Garcias Pass, *H. Bolus s.n.* (BOL).

33.23 (Uniondale): 8 km W of Avontuur (CA), *Gillett 1605* (BOL).

34.18 (Simonstown): S slopes Helderberg (BB), *Galpin 12312* (PRE). Sir Lowrys Pass, *Leighton 823* (BOL, PRE); *Lewis 973* (GRA, SAM); *Barker 3373* (NBG).

34.19 (Caledon): Botrivier (AA), *Zeyher 4085* (SAM). Caledon (AB), *Guthrie s.n.* (BOL-17857). Hermanus (AC), *H. Bolus 9830* (BOL); *Goldblatt 3010*. Riviersonderend (BB), *Zeyher 4083* (SAM).

34.20 (Bredasdorp): Storms Vlei (AA), *Galpin 4652* (GRA, PRE); *Leipoldt 3568* (BOL); *Dymond s.n.* (BOL-21240). Bontebok Park, Swellendam (AB), *Grobler 465* (PRE). Oysterbeds Hotel (BD), *Marsh 809* (PRE). Mountain above Bredasdorp (CA), *Barker 10852* (NBG). Bredasdorp, *Loubser 392* (BOL).

34.21 (Riversdale): 8 km S of Riversdale (AA), *Lewis 5634* (NBG). Near Riversdale, *Muir 1224, 2677* (both BOL).

34.22 (Mossel Bay) Great Brak River (AA), *Burchell 6150, 6202* (both K); *Lewis 5602* (NBG, PRE). Above Victoria Bay (BA), *Lewis 3576* (SAM); *Barker 8179* (NBG).

34.24 (Humansdorp): Oudebosch flats (AA), *Fourcade 3361* (BOL), *961* (BOL, GRA).

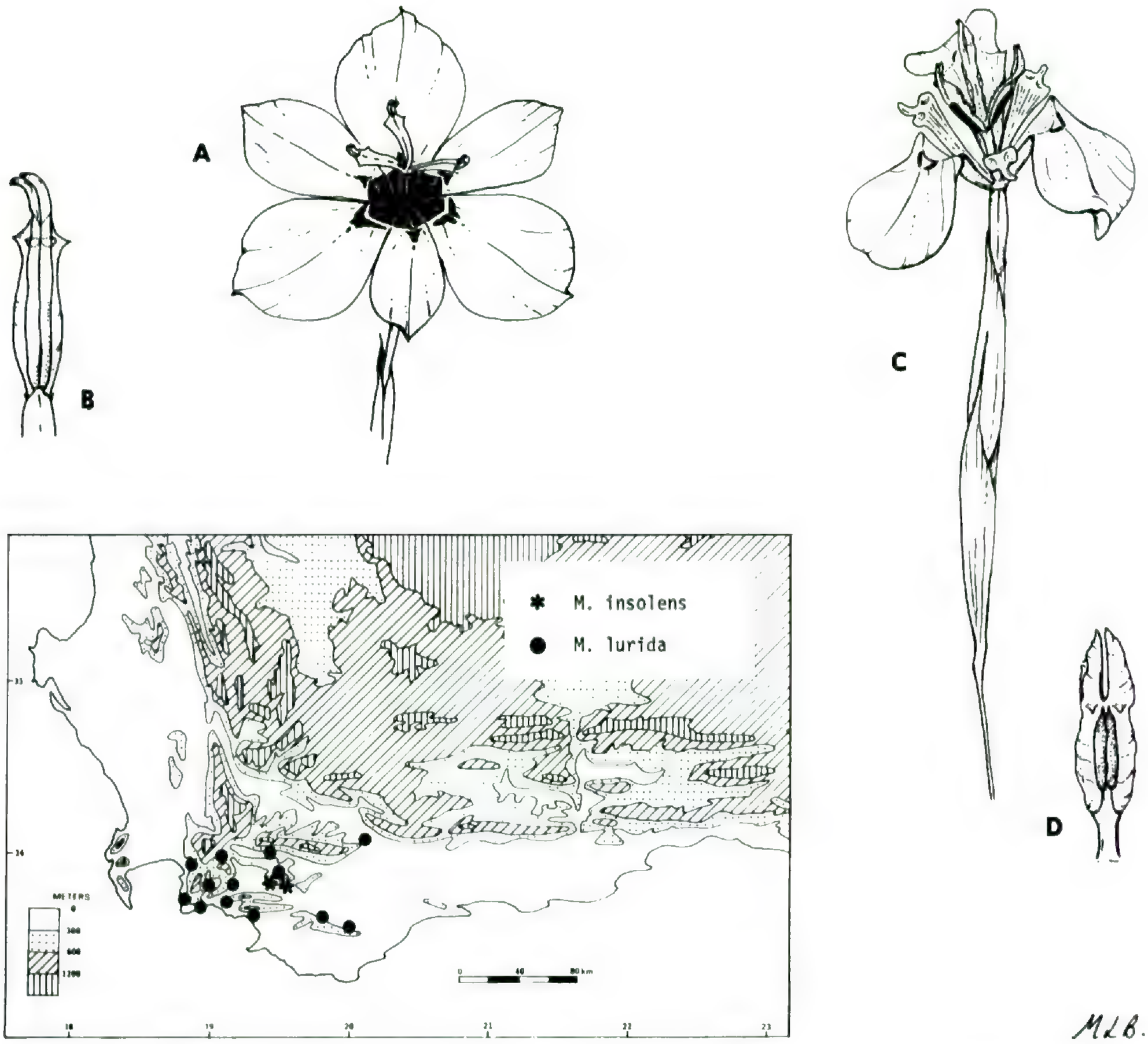


FIGURE 31. Morphology and distribution of *Moraea insolens* and *M. lurida*.—A–B. *M. insolens*.—A. Flower (life size).—B. Style branch and anther enlarged.—C–D. *M. lurida*.—C. Flower (life size).—D. Style branch and stamen enlarged.

42. **Moraea lurida** Ker, Bot. Reg. *tab. 312*. 1818. TYPE: Illustration in Bot. Reg. *tab. 312*.—FIG. 31C–D.

Vieusseuxia lurida (Ker) Sweet. Hort. Brit., ed. 1. 395. 1825.
Phaianthes lurida (Ker) Raf., Fl. Tell. 4: 30. 1838.
Moraea montana Schlecht., Bot. Jahrb. Syst. 27: 92. 1900. TYPE: South Africa, Cape, Onrus R. mouth, *Schlechter 9494* (B, lectotype; BOL, GRA, K, PRE, isolectotypes).
M. fusca Baker, Bull. Misc. Inform. 1906: 42. 1906. TYPE: South Africa, Cape, Caledon, *Penther 762* (K, holotype; BOL, isotype).

Plants 20–30 cm high, often branched. *Corm* 1–1.5 cm in diameter with tunics of coarse, often woody fibers. *Leaf* solitary, basal, linear, glabrous, exceeding the inflorescence. *Stem* glabrous, the branches held away from the axis. *Spathes* herbaceous with dry attenuate apices; inner spathe (3.5–)4–5.5(–7.0) cm long, the outer ca. half the inner. *Flowers* often a livery maroon color, or partly to entirely yellow to cream, usually bad smelling; outer tepals 2.2–3.0 cm long with a broad claw 1.3–1.7 cm long, the claw broadest below the knee and narrowed at the apex, lightly papillate, the limb ca. 1 cm wide, spreading to reflexed; inner tepals either entire, becoming apiculate, or ± 3-lobed at the apex, 1.2–1.5 cm long, with a distinct broad claw and spreading limb. *Filaments* ca.

6 mm long, joined almost to the apex; *anthers* 4–6(–8) mm long, apiculate. *Style branches* to 6 mm long, ca. 2 mm wide, the crests 2–3 mm long, triangular. *Capsule* clavate, to 1.5 cm long; *seeds* many, angular. Chromosome number $2n = 12$.

Flowering time: October to November.

Distribution: Sandy flats and lower mountain slopes, from Sir Lowrys Pass to Bredasdorp.—Fig. 31.

Moraea lurida is very common on sandy mountain soils throughout the Caledon district. It is, however, rarely seen except a year or two after a veld fire when it appears in large numbers on recently burnt slopes. The species is extremely variable in flower color and to some extent in form. Typically the flower is a dark liverish red, and smells faintly of bad meat; other colors range from red marked with yellow, through orange, violet, brown to cream and white. The lighter colored forms do not seem to smell, yet are equally attractive to flies which visit *M. lurida* in large numbers and are probably the principal pollinators. Individual populations are usually relatively uniform in color, but the whole range of known colors has been observed in some places. The shape of the inner tepals varies from fairly broad and entire to truly tricuspidate with a fairly long coiled central cusp.

Moraea lurida is allied to *M. insolens*, a very local species with extremely large anthers, occurring near Caledon and to the widespread, white-flowered *M. tricuspidata*. Confusion is possible between the light colored forms of *M. lurida* and *M. tricuspidata*. While it is sometimes difficult to tell the two apart, *M. lurida* is distinguished by its preference for sandy habitats, grey to black corm tunics, beardless, but minutely papillate tepals, and red orange pollen.

South Africa. cape: 34.18 (Simonstown): Foot of Sir Lowrys Pass (BB), *Lewis 3575* (SAM). Near Prinkle Bay (BD), *Compton 20072* (NBG). Bettys Bay, *Ebersohn s.n.* (NBG-92594). Arieskraal, *Barker 3363* (NBG). Eksteens Kloof, Kogelberg Reserve, *Boucher 925* (PRE, STE).

34.19 (Caledon): Houwhoek Pass (AA), *Barnard s.n.* (BOL-20851, K, PRE, SAM); *Werdermann & Oberdieck 157* (PRE). Foot of Viljoens Pass, *Goldblatt 2491* (MO, PRE). Caledon (AB), *Penther 762* (BOL, K). Zwartberg, *H. Bolus 8489* (BOL, K); *Bodkin s.n.* (BOL); *Schlechter 5530* (BOL, BR); *Galpin 4644* (GRA, K, PRE). Slopes near Hermanus (AC), *H. Bolus 9332* (BOL, GRA); *Goldblatt 674* (BOL). Onrus R. mouth, *Schlechter 9494* (B, BOL, GRA, PRE). Genadendal (BA), *Pappe s.n.* (SAM-70704); *Marloth 7102* (PRE). Dasberg near Storms Vlei (BB), *Stokoe s.n.* (SAM-59818).

34.20 (Bredasdorp): Bredasdorp (CA), *Breach s.n.* (BOL); *Frowein s.n.* (PRE); Springfield Estates, *Stokoe s.n.* (SAM-60095).

43. **Moraea insolens** Goldbl., Fl. Pl. Africa. *tab. 1639*. 1971. type: South Africa, Cape, Caledon district, Drayton siding, *Goldblatt 570* (BOL, holotype; K, PRE, isotypes).—Fig. 31A–B.

Homeria maculata Klatt, Linnaea 34: 628. 1863, pro parte. type: South Africa, Cape, Caledon district, "Boontjeskraal" near Zwartberg, *Ecklon & Zeyher 259* (B, lectotype; S, isolectotype); excl. paratype *Ecklon & Zeyher Irid. 38* (B) coll. "Langehoogde," Caledon district = *Homeria*.

Plants medium tall, to 35 cm high, growing in small clumps. *Corm* ca. 1 cm in diameter; tunics brown, of coarse fibrous layers, extending upwards in a neck. *Leaf* solitary, linear, canaliculate, usually exceeding the inflorescence. *Stem* usually branched. *Spathes* herbaceous with dry scarious apices; inner spathe 5–6 cm long, the outer 3–4 cm. *Flowers* up to 5 cm in diameter, either bright

orange or creamy yellow, marked in the center with brown; outer tepals ca. 3 cm long, and to 2 cm wide, poorly differentiated into limb and claw; inner tepals similar to the outer but smaller, to 2.5 cm long, 1.5 cm wide. *Filaments* ca. 4 mm long, free towards the apex; *anthers* ca. 8 mm long, exceeding the style crests, the pollen orange. *Style branches* 4 mm long, narrow, the crests short, triangular. *Capsule* clavate, *seeds* angled, small. Chromosome number $2n = 12$.

Flowering time: Late September and October.

Distribution: Clay and gravel soil on the southern slopes of the Caledon Zwartberg.—FIG. 31.

This unusual and extremely attractive species grows in clay and gravelly soil and is known only from the southern slopes of the Zwartberg at Caledon. Although very conspicuous when in flower, it has been recorded only rarely; the reason is evidently that, like its close ally *Moraea lurida*, it flowers well only after a fire. The robust many-branched plants produced in the first season after a fire give way subsequently to smaller, fewer-branched plants in the following years, and by the fourth season few if any plants come into bloom.

Apart from specimens obtained at the Caledon Wild Flower Show, there are few collections of *M. insolens*, and these are from only three localities, all near Caledon. Plants collected by Guthrie (BOL-17858) have cream flowers which are marked much as the typical orange form. *Moraea insolens* is believed to be closely related to *M. lurida*, a common species in the Caledon area, which is found only on sandy soils. *Moraea insolens* is, however, quite distinct, having a larger flower, rather differently proportioned tepals with shorter claws, and very distinctive long anthers, much exceeding the stigma lobes, a feature known in several other species, notably *M. gigandra*. This character has clearly arisen independently in the genus, as species with this feature are not closely related.

At the present time only one population is known, from the type area. At this site, only about one acre in extent, most plants were destroyed when a tiny plot was ploughed up and planted to wheat. Adjacent to the wheat field, several plants were discovered, and these, at present under no protection, could well be exterminated at any moment.

Only after *M. insolens* had been described did it become evident that *Homeria maculata* might be a synonym. The name *H. maculata* has long been applied to a form of *H. elegans* (Jacq.) Sweet with orange outer tepals but is actually based on two elements. The description applies to an orange-flowered plant with ovate-rotund outer tepals, marked green at the base; though known forms of *M. insolens* have brown markings, this color comment cannot be taken at face value since Klatt was describing dry plants collected forty years before. Specimens matching Klatt's description, and bearing Ecklon and Zeyher's manuscript name, *Vieusseuxia aurantiaca* at the Riksmuseum in Stockholm and at the Berlin-Dahlem Herbarium are undoubtedly *M. insolens*; the Berlin collection is selected as the lectotype. As *M. maculata* Sessé and Mociño (= *Tigridia*) blocks the transfer of Klatt's species to *Moraea*, no change in the nomenclature is necessary.

SOUTH AFRICA. CAPE: 34.19 (Caledon): "Boontjeskraal near Zwartberg" (AB), *Ecklon & Zeyher* 239 (B, S). 1 km W of Caledon, *Guthrie s.n.* (BOL-17858, K). Between Caledon

Baths and "Bredekamps Platz" at Steenboksrivier, *Ludwig & Beil sub Ecklon* (S). Drayton siding, E of Caledon (BA), *Barnard s.n.* (NBG-87509); *Barnard & Mauve 4703* (PRE); *Goldblatt 570* (BOL, K, PRE).

Without locality: Caledon Wild Flower Show 1912, Anon (BOL); 1931, comm. *Pillans s.n.* (BOL-30677).

44. **Moraea tricuspidata** (L.f.) Lewis, J. S. African Bot. 14: 89. 1948, name misapplied to *M. aristata* (as *M. glaucopis*).—Fig. 32A–B.

Iris tricuspidata L.f., Suppl. Pl. 98. 1781. TYPE: Several specimens belong to different species cited; origin of the lectotype probably foothills of Devils Peak, Cape Peninsula, *Thunberg s.n.* (Herb. Thunberg 1183, UPS, lectotype).

Iris tricuspis Thunb., Diss. Irid. no. 15. 1782. TYPE: As for *Iris tricuspidata.*

Vieusseuxia tricuspis (Thunb.) Spreng., Syst. Veg. 1: 165. 1825.

Moraea tricuspis (Thunb.) Ker, Bot. Mag. *tab. 696.* 1803; Baker, Fl. Cap. 6: 25. 1896, pro parte.

M. confusa Lewis, J. S. African Bot. 14: 89. 1948. TYPE: Illustration in Bot. Mag. *tab. 696.* 1803.

M. bellendenii subsp. *cormifera* Goldbl., Ann. Missouri Bot. Gard. 61: 236. 1973. TYPE: South Africa, Cape, Atherstone area, Albany distr., *Jacot-Guillarmod 6706* (GRA, holotype; RUH, isotype).

Plants 25–60 cm high, usually several branched. *Corms* 1–2 cm in diameter; tunics pale to dark brown, the fibers medium to coarse. *Leaf* solitary, basal, glabrous, 4–7 mm wide, exceeding the inflorescence and often trailing. *Stem* simple or more often branching from the upper nodes, the branches slender and held away from the axis. *Spathes* herbaceous, occasionally brown above with attenuate apices; inner spathe 4–7 mm long, the outer ca. half the inner. *Flowers* white, speckled at the center, the nectar guide usually brown to yellow, speckled; outer tepals 2.6–3.0 cm long, the claw slightly more than half the total length, 3–5 mm wide at the midpoint, pubescent, the limb ca. 1.5 cm wide, spreading; inner tepals trifid, to 1.2 cm long, excluding the central cusp, ca. 4 mm wide below the point of forking, the lateral lobes obtuse, the inner slender and coiled spirally inwards, 3–5 mm long. *Filaments* 6–7 mm long, free in the upper half; *anthers* ca. 5 mm long. *Style branches* 6–7 mm long, the crests usually 5–7 mm long. *Capsule* clavate, 1.5–2.2 cm long; *seeds* angled. Chromosome number $2n = 12, 24$.

Flowering time: (September) October to mid November.

Distribution: Lower mountain slopes, usually on heavy clay soils, extending from the Cape Peninsula as far east as Grahamstown; most common after fires.—Fig. 32.

This comparatively widespread species is common on the Cape Peninsula and it was here that Thunberg first collected it in the 1770s. Typification of *Moraea tricuspidata* has presented several problems, for Thunberg, in addition to a detailed description, cites several varieties and three localities. There are also several specimens annotated "tricuspis" in the Thunberg collection at Uppsala and these comprise four different species, *M. tricuspidata* = 1183, *M. villosa* = 1184, *M. glaucopis* = 1181 and 1182, and probably *M. bellendenii* = 1185A.

The detailed description given by Thunberg of *Iris tricuspis* upon which the younger Linnaeus based his *I. tricuspidata*, clearly refers to a white-flowered species with tricuspidate inner tepals. The outer tepals are described as hav-

ing a yellow, black-spotted claw and suborbicular, white limb, while the inner tepals are brown spotted, with a trilobed limb, the inner lobe of which is a little longer than the outer ones. This description can only match the specimen numbered 1183 in the Thunberg collection, i.e., the common Cape Peninsula to Grahamstown species named by Lewis, *M. confusa*. Lewis associated the Thunberg species with *M. aristata* (= *M. glaucopis*), the rare white-flowered species with a conspicuous blue and yellow mark on its outer tepals and quite different inner tepals which though tricuspidate, have a long central cusp. With the revised interpretation of *M. tricuspidata*, *M. confusa* falls into synonymy.

The identity of Thunberg's "varieties" is not readily resolved, owing mainly to the peculiar way in which he lists them, so that it is not even clear how many he wished to recognize. Certainly, however, *M. bellendenii* "var. *flava*" and *M. villosa* "var. *purpurea*" are included, both being represented in his herbarium (numbers 1185A and 1184). Probably *M. aristata* is the "var. *alba*," numbers 1181 and 1182 in the collection. The remaining specimen, 1183, is *M. tricuspidata* and is chosen as lectotype. Brown's (1928) statement that the type is in the Smith Collection, sent there by Thunberg in 1791, does not seem likely for there is no reason to suppose this a type, above those still at Uppsala, especially as Brown says it has conspicuous blue markings on the petals and therefore does not conform to the description.

Moraea tricuspidata is closely allied to *M. bellendenii* and is barely distinguishable from it without knowledge of flower color, the flowers of *M. tricuspidata* being white and those of *M. bellendenii* yellow. However, slight but apparently consistent differences in size of floral parts can usually be relied upon to give a correct determination. The two species are undoubtedly distinct for they have different habitat preferences. *Moraea tricuspidata* always blooms slightly earlier and typically grows on clay slopes, while *M. bellendenii*, often taller and more branched, prefers sandy situations. Occasionally the two species do grow near one another as at Kloof Nek, Cape Town, and hybrids have been reported. These are said to be intermediate in height and pale yellow in color. It is also occasionally difficult to distinguish *M. tricuspidata* from the white forms of *M. lurida* such as are found on Houw Hoek Pass, but these are usually shorter, have dark corm tunics and invariably occur in sandy mountain soils.

A smaller form of *M. tricuspidata* with brown markings occurs in the extreme east of its range in the Grahamstown area. This was recognized as a distinct subspecies (Goldblatt, 1973) and was mistakenly assigned to *M. bellendenii* as subsp. *cormifera*. Though somewhat different from forms occurring further west, it is not given taxonomic recognition here and thus is reduced to synonymy.

Moraea tricuspidata is unusual in being heteroploid. Two populations from the eastern part of its range are tetraploid, including the distinct Grahamstown variant, while plants from a population on the Cape Peninsula are diploid, $2n = 12$. Further counts are necessary from populations over the entire range of the species before the significance of this can be assessed.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Signal Hill, Cape Peninsula (CD), *Goldblatt 237* (BOL). Camps Bay, *Zeyher s.n.* (SAM-20603). Slopes of Devils Peak Cape Peninsula, *H. Bolus 4004* (BOL); *Wolley Dod 1742* (BOL, K). Kirstenbosch, Herbarium hill,

Barker s.n. (BOL); *Mauve s.n.* (PRE). Table Mountain, *Ecklon 821* (PRE). Swartboskloof, Jonkershoek (DD), *Lewis 1653* (BOL, SAM-58945). Foot of Victoria Peak, Jonkershoek, *Garside 1710* (K). Heldberberg, Stellenbosch, *Gillett 1798* (STE).

33.19 (Worcester): Laken Vlei (BC), *Olivier s.n.* (BOL, NBG-58896). French Hoek Pass (CC), *Barker 4150.*

33.23 (Willowmore): Lauterwater, Long Kloof (DC), *Fourcade 5022* (K).

33.24 (Steytlerville): Near Kareedouw (CD), *Goldblatt 2861* (MO, NBG). Twee Rivieren, Long Kloof (DC), *Fourcade 1722* (BOL, GRA).

33.25 (Port Elizabeth): Bakens River valley (DC), *Cruden 399* (GRA).

33.26 (Grahamstown): Atherstone area (BC), *Jacot-Guillarmod 6706* (GRA, RUH); *Goldblatt 2865* (K, MO, PRE, NBG). Grahamstown brickfields, *Daly & Cherry 41* (GRA); *Dyer 1661* (GRA, K).

34.18 (Simonstown): Hout Bay (AB), *Bond 1225* (NBG); *Lewis 52* (SAM).

34.24 (Humansdorp): Jeffrey's Bay (BB), *Goldblatt 2893* (MO).

Without precise locality: *Sparrman 3133* (S).

45. **Moraea bellendenii** (Sweet) N. E. Brown, Bull. Misc. Inform. 1929: 139. 1929.—Fig. 32C.

Vieusseuxia bellendenii Sweet, Hort. Brit., ed. 1. 395. 1827. TYPE: Illustration in Bot. Mag. *tab. 772.* 1803.

Moraea tricuspis (Thunb.) Ker var. *lutea* Ker, Bot. Mag. *tab. 772.* 1803. TYPE: Illustration in Bot. Mag. *tab. 772.* 1803.

M. pavonia (L.f.) Ker var. *lutea* (Ker) Baker, Fl. Cap. 6: 24. 1896.

Vieusseuxia spiralis de la Roche, Diss. 31. 1766. TYPE: Illustration in de la Roche, Diss. *tab.* 5. 1766.

Plants slender, 50–100 cm high, usually several branched. *Corms* 1.5–2 cm in diameter; tunics pale brown, of medium to coarse fibers. *Leaf* solitary, basal, linear, glabrous, to 1 cm wide, exceeding the inflorescence but trailing. *Stem* ± erect, branching at the nodes, the branches slender, ± upright. *Spathes* herbaceous, brown above, the apices attenuate; inner spathe 5–7 cm long, the outer ca. half this length. *Flowers* yellow, speckled in the center; outer tepals 2.2–3.3 cm long and up to 3 cm wide, the claw 0.9–1.3 cm long, very broad, veined and speckled, the limb 1.4–1.8 cm wide, ca. as long as wide, outspread to ascending; inner tepals trifid, 0.8–1.0 cm long excluding the inner cusp, usually ca. 4 mm wide at the point of forking, the lateral lobes short and obtuse, the inner slender, 2–4 mm long and coiled obliquely inward. *Filaments* 3–5 mm long, free for the upper 1 mm; *anthers* 4–5 mm long. *Style branches* ca. 6 mm long, crests 3–5(–8) mm, narrowly triangular. *Capsule* clavate, ca. 1.5 cm long; *seeds* many, angular. Chromosome number $2n = 12$.

Flowering time: October to November.

Distribution: Sandy slopes and flats in coastal areas from the Darling district in the west to Knysna and Plettenberg Bay in the east; rarely on clay.—Fig. 32.

Moraea bellendenii is a common species along the Cape coast from the vicinity of Darling in the west to Plettenberg Bay in the east. It shows a marked preference for very sandy situations, though is occasionally found on clay. It is very closely allied to *M. tricuspidata*, and it is often difficult to distinguish the two when dry, as color is an important difference, *M. bellendenii* being bright yellow and *M. tricuspidata* white to cream colored. Small differences in size of floral parts can also be used as an aid to identification (see discussion of *M. tricuspidata*). *Moraea tricuspidata* has the same general distribution though it ex-

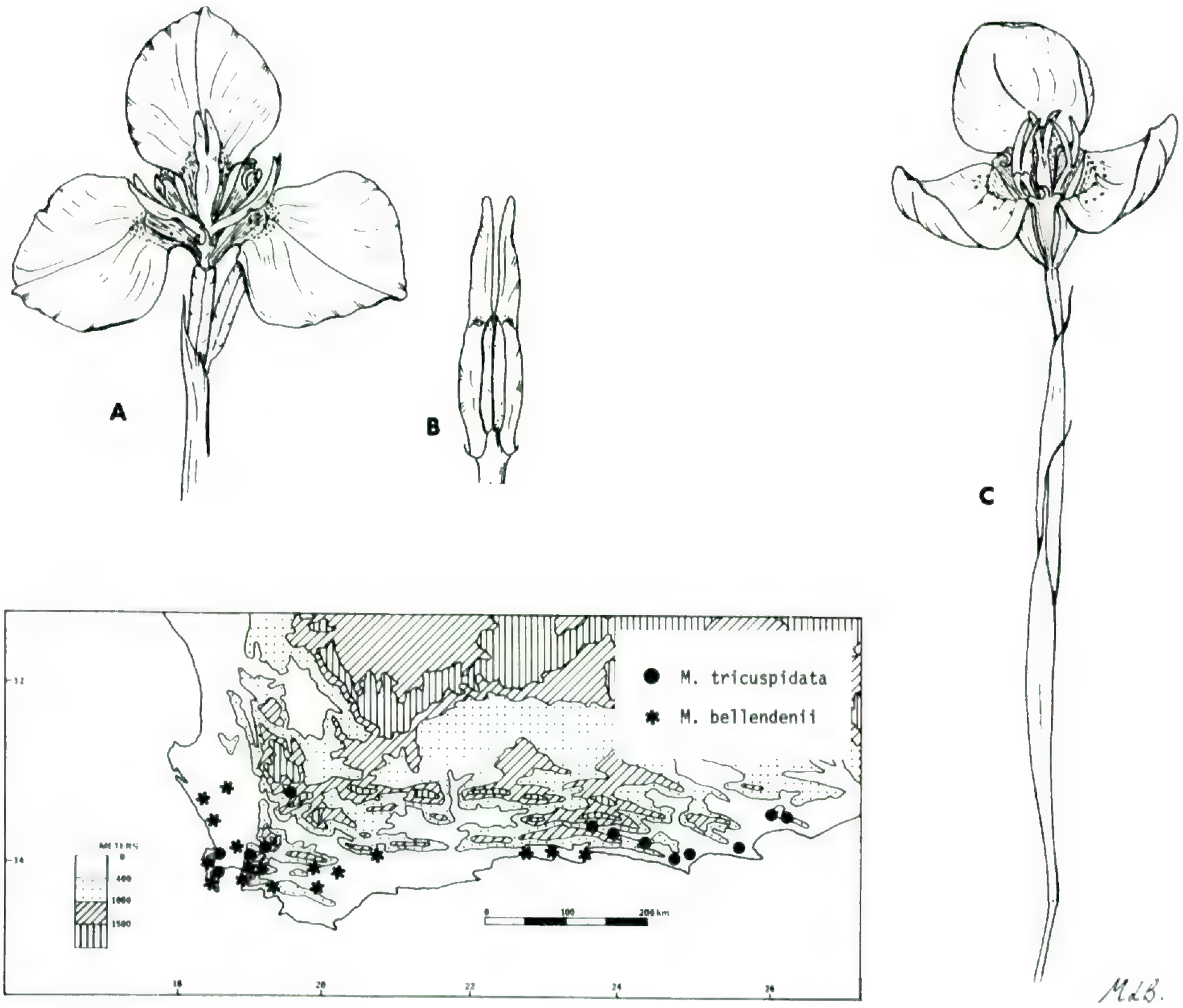


FIGURE 32. Morphology and distribution of *Moraea tricuspidata* and *M. bellendenii*.—A–B. *M. tricuspidata*.—A. Flower (life size).—B. Style branch and anther (×2).—C. *M. bellendenii*. Flower (life size).

tends further inland and also further east, as far as Grahamstown, and is found predominantly on clay soils.

Moraea bellendenii subsp. *cormifera* Goldbl. described recently (Goldblatt, 1973) from the Grahamstown area was misplaced under *M. bellendenii* and after a study of living plants, I have concluded that it is no more than a form of *M. tricuspidata*.

Moraea bellendenii was one of the first species of *Moraea* to be described, as *Vieusseuxia spiralis* de la Roche, and is the lectotype of *Vieusseuxia*. *Moraea spiralis* L.f. (= *Aristea*), however, bars the transfer of *V. spiralis* to *Moraea*.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Mamre hills (AD), *Wasserfall 439* (NBG, STE). Waylands, Darling, *Barker 720* (BOL, NBG). Oudepos, Darling, *Barker 10786* (NBG). Hills round Darling, *Bolus s.n.* (BOL). Near Moorreesburg (BA), *Bolus 9987* (BOL). Lions Head, Cape Peninsula (CD), *Bolus 8024* (BOL, GRA); *Tyson 2485* (SAM); *Levyns s.n.* (SAM-52930); *MacOwan in Herb Aust. Afr. 1965* (BOL, SAM, UPS). Camps Bay, Cape Peninsula, *Wolley Dod 3138* (BOL); *Marloth 234* (BOL); *Cassidy 249* (NBG); *Lewis 940* (SAM). Tygerberg, Bellville (DC), *Barker 8436* (NBG). Sewefontein, above Kuils River, *Oliver 4724* (STE). Joostenberg (DD), *Esterhuysen 15985* (BOL, NBG); *Lewis 5905* (NBG). Uitkyk hill, Stellenbosch, *Gillett 1829* (STE).

33.19 (Worcester): Near Laken Vlei (AC), *Phillips 2067* (SAM).

34.18 (Simonstown): Llandudno, Cape Peninsula (AB), *Lewis 941* (SAM); *Barker 3237* (NBG). Kogel Bay (BB), *Werdermann & Oberdieck 287* (PRE).

34.19 (Caledon): Elgin (AA), *L. Bolus s.n.* (BOL-19149). Houw Hoek, *Schlechter 2584* (PRE). Near Hawston, Bot R. valley, *van Niekerk 802* (BOL); *Goldblatt 676* (BOL). Caledon (AB), *Ecklon s.n.* (S); *Leipoldt 3567* (BOL). Near Onrust (AC), *Gillett 4400* (BOL). Greyton (BA), *Bayliss 4015* (BOL, NBG, MO). Rivier Zonder End (BB), *Barker 1337* (NBG); *Zeyher 4081* (K, S, SAM).

34.20 (Bredasdorp): Suurbraak, near Tradouw Pass road (BA), *Lewis 5652* (NBG).

34.22 (Mossel Bay): Near Belvedere Church, Knysna (BB), *Duthie 1137* (BOL). Ruigte vlei, *Fourcade 1554* (BOL, GRA, PRE).

34.23 (Knysna): Leisure Isle, Knysna (AA), *Cassidy 220* (NBG). Near Keurbooms River, Plettenberg Bay (AB), *Mauve 4570* (PRE); *Goldblatt 2911* (MO).

46. **Moraea neopavonia** Foster, Contr. Gray Herb. 165: 107. 1947, nom. nov. pro *M. pavonia* (L.f.) Ker. TYPE: As for *Iris pavonia* L.f.—FIG. 33A–C.

Iris pavonia L.f., Suppl. Pl. 98. 1781. TYPE: South Africa, Cape, Swartland hills, *Thunberg s.n.* (Herb. Thunberg 1148A, UPS, lectotype).

Moraea pavonia (L.f.) Ker, Ann. Bot. (König & Sims) 1: 240. 1805; Baker, Fl. Cap. 6: 23. 1896, excl. vars., hom. illeg., non *M. pavonia* (L.f.) Thunb., 1787.

Vieusseuxia pavonia (L.f.) DC., Ann. Mus. Natl. Hist. Nat. 2: 139. 1803.

Plants slender, 30–60 cm high. *Corms* ca. 1 cm in diameter; tunics brown, the inner fibers fine, the outer coarse. *Leaf* solitary, basal, linear, sparsely pubescent on the outer surface, exceeding the inflorescence. *Stem* finely pubescent, simple or 1-branched. *Spathes* herbaceous below, dry above with long, dark brown, attenuate apices; inner spathe 4.5–7(–8) cm long, the outer ca. ⅔ the length of the inner. *Flowers* orange, marked with a navy blue to green nectar guide and often speckled in the center; outer tepals 2.2–4.0 cm long, the limb 1.5–3 cm long, broadly ovate, to 2–3 cm wide, spreading; inner tepals 1.5–2.5 cm long, ± outspread, entire and narrowly lanceolate or weakly to distinctly trifid with 2 small obtuse lateral lobes and a long central cusp. *Filaments* ca. 4 mm long, free in the upper 1 mm; *anthers* ca. 1 cm long, exceeding the style crests. *Style branches* 5 mm long, the crests 1–2 mm, triangular. *Capsule* cylindrical, 2–4 cm long; *seeds* angled, with spongy, inflated testa. Chromosome number $2n = 12$.

Flowering time: Late September.

Distribution: Gravelly clay slopes and flats near the Berg River between Paarl and Piketberg.—FIG. 33.

The very striking *Moraea neopavonia* is a rare species, known today from only two localities. It was probably never common, but was certainly more widespread in the past. Its recorded range extends along the Berg River from near Paarl to beyond the Piketberg, an area now intensely cultivated and relict stands occur only on stony patches or steep banks. In view of its great beauty and potential for horticulture, the species should be protected from further extension of agriculture into its last remaining habitats.

Moraea neopavonia is one of several species in which the inner tepals vary from entire to tricuspidate. The entire condition is presumably ancestral and the occurrence of this feature places *M. neopavonia* at the beginning of the "peacock" group of species, those with brightly colored, very broad outer tepals and conspicuous nectar guides. In *M. neopavonia*, the bright orange to red flowers

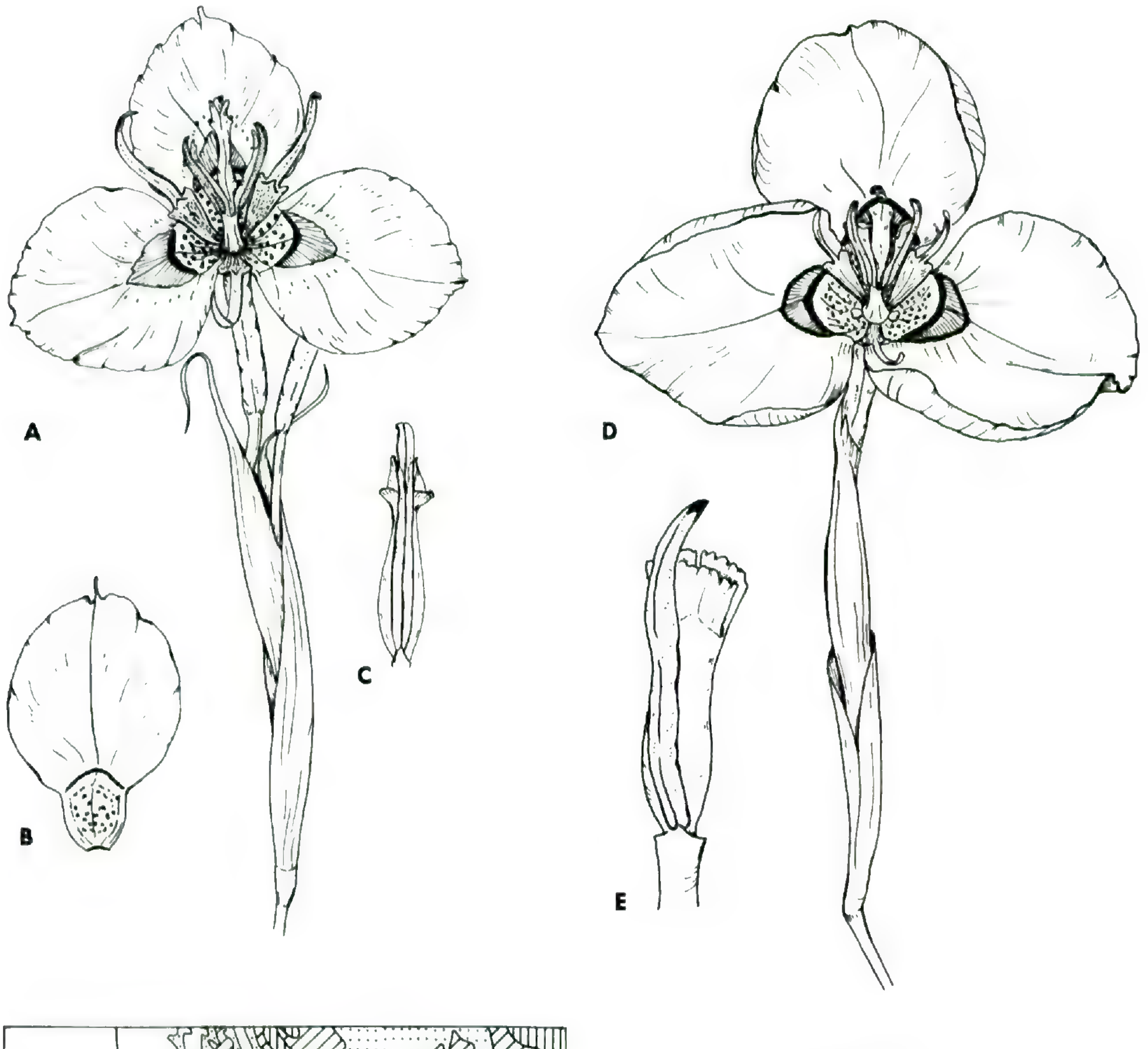


FIGURE 33. Distribution and/or floral morphology of *Moraea neopavonia*, *M. gigandra*, *M. caeca*, and *M. amissa*.—A–C. *M. neopavonia*.—A. Flower (life size).—B. Tepal (life size).—C. Style branch and anther (enlarged).—D–E. *M. gigandra*.—D. Flower (life size).—E. Style branch and stamen (enlarged).—F–G. *M. caeca*.—F. Flower (life size).—G. Style branch and stamen (enlarged).

are marked with navy blue or peacock green. Apart from its unusual flower color, the species is distinctive in having very large anthers which exceed the stigmas and style crests.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Banks of Berg River near Piketberg (DC), *Schlechter 5263* (BOL, K, NBG, PRE). Near Berg River bridge (DD), *Salter 3666* (BOL, K); *Barnard s.n.* (BOL, K); *Goldblatt 654* (BOL).

33.18 (Cape Town): NE slopes of Heuningberg near Halfmanshof (BB), *Goldblatt 655, 685* (both BOL, MO). Near the potteries at Paarl (DD), *Middlemost 1714* (NBG).

33.19 (Worcester): Hermon–Tulbagh road (AC), *Mauve 4647* (PRE).

Without precise locality: Cape, *Thunberg s.n.* (S, UPS).

47. **Moraea gigandra** L. Bol., S. African Gard. 17: 418. 1927. TYPE: South Africa, Cape, precise locality unknown, *Metelerkamp s.n.* (BOL, holotype). —FIG. 33D–E.

Plants 20–40 cm high, usually unbranched. *Corms* ca. 1.5 cm in diameter; tunics of fine inner fibers and coarse woody outer fibers. *Leaf* solitary, basal, linear, sparsely pubescent or glabrous, equal to or exceeding the inflorescence. *Stem* finely pubescent, simple or bearing 1 branch. *Spathes* herbaceous below, dry above with dark brown attenuate apices; inner spathe 5–8 cm long, the outer 3–5 cm. *Flowers* large, purple, white or cream with a dark, narrow nectar guide; outer tepals 3–4.5 cm long with a broad, short claw ca. 6 mm long and a very broad spreading limb, ca. 3.5 cm wide; inner tepals 0.9–1.5 cm long, tricuspidate with 2 short lateral lobes and a longer, ± outspread central cusp. *Filaments* 2–4 mm long, free near the apex; *anthers* very large, 1.3–1.5 cm long, much exceeding the style crests. *Style branches* ca. 6 mm long, 2 mm wide, the crests minute, barely exceeding the large stigma lobe. *Capsule* 2–3 cm long, cylindrical; *seeds* unknown. Chromosome number $2n = 12$.

Flowering time: Late September, October.

Distribution: Clay soils, in the plains between the Piketberg and the Olifants River Mountains, north of the Berg River.—FIG. 33.

Once common north of the Berg River in the broad valley between the Piketberg and Olifants River Mountains, *Moraea gigandra* is now on the verge of extinction. Its habitat, the rich clay soil of this area, is now almost entirely given over to grain cultivation, and it survives in only a few isolated places, unsuitable to the plough.

Moraea gigandra has one of the largest and most striking flowers in the genus, with the broad shortly clawed outer tepals as long as 4.5 cm. Blue purple flowers are most frequent, but white and cream forms also occur. The flowers are distinctive not only in size, but also for their extraordinarily long anthers which reach 1.5 cm in length, much exceeding the stigma. The style crests are barely developed and are about as long as the stigmatic lip.

This comparatively late-flowering species was only brought to the attention of science in 1927, though it was evidently known in Europe in the eighteenth century. A manuscript description in the hand of Daniel de la Roche, who described the genus *Vieusseuxia*, attests to this little known fact (Goldblatt & Barnard, 1970). Today *M. gigandra* is cultivated by a few people in South Africa and also in New Zealand where it thrives.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Near Piketberg (DD), *H. Bolus 13654* (BOL). Piketberg, *Hofmeyr s.n.* (BOL-17546); *van der Spuy 39* (BOL); *Lewis Grant 3465* (MO). 4 km N of Piketberg on road to Pools, *L. Bolus s.n.* (BOL-31296). Hilltop near Berg River bridge, *Barnard 241* (BOL). Nurust farm 10 km N of Porterville, ca. 8 km from the mountains, *Loubser 2105* (BOL, NBG).

48. **Moraea caeca** Barnard ex Goldbl., Ann. Missouri Bot. Gard. 63: 21. 1976. TYPE: South Africa, Cape, top of Dasklip Pass near Porterville, *Goldblatt 678* (BOL, holotype; K, MO, PRE, S, isotypes).—FIG. 33F–G.

Plants slender, 20–40 cm high. *Corm* ca. 1 cm in diameter; the tunics light brown, fibrous. *Leaf* solitary, linear, glabrous, exceeding the inflorescence. *Stem* glabrous, occasionally pubescent, occasionally 1-branched, the branches held close to the axis. *Spathes* herbaceous or dry above with brown attenuate apices; inner spathe ca. 5 cm long, the outer to ca. 2.5 cm. *Flowers* mauve lilac with a small yellow or black nectar guide; outer tepals spreading, 2.3–2.8 cm long with an erect, channelled, pubescent claw 8–12 mm long and a broadly ovate, spreading limb, to 1.8–2.2 cm wide; inner tepals tricuspidate, channelled, the central cusp 5–8 mm long, the laterals to 2 mm. *Filaments* 2–3 mm long, united at least in the lower half; *anthers* dark, ca. 5 mm long. *Style branches* ca. 5 mm long, the crests acute to obtuse, to 7 mm long. *Capsule* clavate, to 1.5 cm; *seeds* angular. Chromosome number $2n = 12$.

Flowering time: Late September and October.

Distribution: Found only in mountainous areas in the Piketberg and Twenty Four Rivers Mountains as well as locally on the Cape Peninsula.—FIG. 33.

Though clearly a member of the "peacock" alliance, *Moraea caeca* lacks the conspicuous nectar guide characteristic of the group. Instead of the usual dark crescent surrounding a yellow "eye," the nectar guide is most often a small black dot. The tepals are also less brightly colored than other species in the group, being a plain pale lilac mauve. *Moraea caeca* is the only species in the group that has a montane distribution, and it occurs on sandy soils on the Piketberg, the mountains above Porterville, and locally on the Karbonkelberg on the Cape Peninsula.

Typically the stem and leaves are quite glabrous, but a collection from the Groot Winterhoek (*Haynes* 858) is conspicuously villous. The flowers of this collection are somewhat larger than the usual, but otherwise conform in color and marking to other populations. *Moraea caeca* is probably most closely related to *M. villosa* and the rare and almost extinct *M. aristata*, which occur in the lowland areas below the mountains on which *M. caeca* grows.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Kloof on SW side of Piketberg (DC), *Barnard s.n.* (BOL). Moutons Valei, *Marloth 11509* (PRE). Hills NW of Moutons Vlei, *Pillans 7488* (BOL). Piketberg (DD), *Vlok s.n.* (NBG-58948). Beyond Piketberg on Redelinghuys road, *Barnard s.n.* (SAM-52394, BOL).

32.19 (Wuppertal): Dasklip (Cardouw) Pass above Porterville (CC), *Barker 7599* (NBG, STE); *Esterhuysen 16211* (BOL); *Goldblatt 678* (BOL, MO, K, PRE). Mountain above Porterville, *Loubser 856* (NBG).

33.19 (Worcester): Driebosch, Groot Winterhoek (AA), *Haynes 858* (STE).

34.18 (Simonstown): Karbonkelberg, Cape Peninsula (AA), *Salter 3288* (BM).

49. **Moraea aristata** (de la Roche) Aschers. & Graebn., Syn. Mitteleur. Fl. 3: 518. 1906.—Fig. 34A.

Vieusseuxia aristata de la Roche, Diss. 33. 1766. TYPE: South Africa, Cape, exact locality unknown (cult. Europe), *Van Royen s.n.* (Herb. Van Royen, L, lectotype).
V. glaucopis D.C. in Redouté, Lil. *tab. 42.* 1803; Ann. Mus. Natl. Hist. Nat. 2: 141, *tab. 42.* 1803. TYPE: Illustration in Redoubté, Lil. *tab. 42.*
Moraea glaucopis (D.C.) Drapiez,[8] "Encyc. 4" Dict. Class. Sci. Nat. 7: 478. 1841; Baker, Fl. Cap. 6: 23. 1896.
M. candida Baker, Handbook Irid. 59. 1892, nom. nov. pro *Vieusseuxia fugax* de la Roche.
Ferraria ocellaris Salisb., Prodr. Stirp. 41. 1796, nom. nov. pro *Iris pavonia* var. TYPE: Illustration in Bot. Mag. *tab. 168.* 1791.
Moraea tricuspis (Thunb.) Ker var. *ocellata* D. Don, Br. Fl. Gard., ser 2. 3, *tab. 249.* 1834. TYPE: Illustration in Br. Fl. Gard., ser 2. *tab. 249.*

Plants 25–35 cm high. *Corms* ca. 1.5 cm in diameter; tunics of pale fibers. *Leaf* solitary, linear, glabrous, basal, exceeding the inflorescence. *Stem* glabrous, occasionally 1-branched. *Spathes* herbaceous, dry above with dark brown, attenuate apices; inner spathe 5–7 cm long, the outer ca. half the length of the inner. *Flowers* white with prominent nectar guide variously marked with concentric crescents of black, blue violet, or green; outer tepals 3–3.5 cm long, the claw heavily bearded, ca. 1.2 cm long, the limb very broad, spreading, ca. 2 cm long and to 2.5 cm wide; inner tepals 1.5–2 cm long, tricuspidate, the lateral lobes short, obtuse, the central cusp long, spreading. *Filaments* 3–4 mm long, free near the apex only; *anthers* ca. 5 mm long. *Style branches* ca. 7 mm long, the crests 7 mm long, triangular. *Capsule* clavate-cylindrical, 1.5–2 cm long; *seeds* angled, with a spongy testa. Chromosome number $2n = 12$.

Flowering time: September.

Distribution: Known only from the Royal Observatory grounds on the Liesbeek River, Cape Town; in clay soil but more widespread in the past.—Fig. 34.

It is no exaggeration to say that *Moraea aristata* is far more common in European herbaria than it is in the wild, and it is in fact close to extinction. This striking white-flowered, blue-eyed member of the "peacock" alliance was never widespread, and the early records suggest it grew only on clay slopes and flats in the northern Cape Peninsula, between Cape Town and Rondebosch. Today there is little open land here, but *M. aristata* still survives on the grounds of the Royal Observatory in Cape Town, along the Liesbeek River. Insufficient individuals remain to constitute a viable population, few plants producing flowers, and less seed.

There is no record of how *M. aristata* reached Europe, but it was in cultivation in Holland during the mid eighteenth century. It was first described in 1766 by Daniel de la Roche, pupil of the famous Dutch botanist Van Royen, who assigned it to the genus *Vieusseuxia*. A printer's error, transposing the epithets of *V. aristata* and a second species *V. fugax* opposite their descriptions in de la Roche's published Dissertation (Goldblatt & Barnard, 1970) subsequently led to some confusion and caused some botanists to reject both species. Although I had in

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[8] This combination is often incorrectly attributed to Baker, e.g., Baker, Handbook Irid. 59. 1892.

the past been uncertain of the identity of *M. aristata* (Goldblatt & Barnard, 1970), close study has removed this doubt.

The species was collected later by Thunberg in the 1770s and specimens in his collection at Uppsala bear the epithet "*tricuspis*." These specimens are probably Thunberg's *Iris tricuspis* var. *alba*, the typical variety which is now recognized under the younger Linnaeus's epithet, *M. tricuspidata* (L.f.) Lewis (see discussion under this species). Lewis (1948), who rejected *M. aristata* on grounds of nomenclatural confusion, identified this species with *M. tricuspidata*, a determination not followed here. The discussion under *M. tricuspidata* deals with this situation in detail.

In the later eighteenth century all the so-called "peacock" moraeas were treated as *Moraea* (or *Vieusseuxia*) *pavonia*: thus *M. aristata* appears in the *Botanical Magazine* under this name. Salisbury recognized the illustration as representing a different species, which he named *Ferraria ocellaris*. Yet another epithet was provided, this time by De Candolle, in 1803, who called the plant *Vieusseuxia glaucopis*, and it is known as *M. glaucopis* today in Europe, where it is occasionally grown for ornament.

Moraea aristata is very closely related to the widespread *M. villosa* but differs not only in flower color and markings, but also in having an entirely glabrous stem and leaf. It is diploid with $2n = 12$, in contrast to *M. villosa* in which only polyploid populations are known.

South Africa. cape: 33.18 (Cape Town): Royal Observatory grounds (CD), *Compton 16041* (NBG); *Leighton 552* (BOL, SAM); *Salter 8488* (SAM); *Adamson 2583* (SAM); *Zeyher 5017* (SAM); *Davis s.n.* (SAM-60132). Foot of Devils Peak, *Thunberg s.n.* (UPS); *Drège s.n.* (GRA): *Pappe s.n.* (S).

Without precise locality: *Oldenburg* (S); *Ecklon* (S); *Thunberg* (C, S, UPS); *Herb. Gay* (K).

50. **Moraea amissa** Goldbl., sp. nov. type: South Africa, Cape, Malmesbury district, 10 km NW of Malmesbury, *Acocks 20739* (PRE, holotype).

Planta gracilis, ad 30 cm alta. *Folium* solitarium basale, canaliculatum. *Caulis* simplex. *Spatha* herbacea, brunnea supra, interiora ca. 4 cm longa, exteriora ca. dimidia. *Flores* violacei; tepala exteriora 1.8–2.0 cm longa, limbus ca. 1.2 cm longus, ad 1.3 cm latus, effusus; tepala interiora ± lanceolata vel ± tricuspidata, ad 1.5 cm longa. *Filamenta* 3–4 mm longa, libera propre apicem, pubescentia ad base. *Rami styli* ca. 5 mm longa, cristae ad 4 mm.

Plants slender, ca. 30 cm high. *Corm* not known. *Leaf* solitary, basal, linear, canaliculate, glabrous, exceeding the inflorescence, 1.5–2 mm wide. *Stem* erect, glabrous, simple. *Spathes* herbaceous with dry upper margins, the apices attenuate, dark brown; inner spathe ca. 4 cm long, the outer ca. half the inner. *Flowers* violet with a darker nectar guide lined with white; outer tepals 1.8–2.0 cm long, the claw ca. 0.8 cm, the limb, outspread, to 1.3 cm wide; inner tepals either entire, ± lanceolate or ± tricuspidate, to 1.5 cm long. *Filaments* 3–4 mm long, free near the apex only, pubescent at the base; *anthers* 4 mm long. *Style branches* ca. 5 mm long, the crests to 4 mm. *Capsule* and *seed* unknown. Chromosome number unknown.

Flowering time: Early October.

Distribution: Local in sandstone outcrop, northwest of Malmesbury.—Fig. 33.

Collected first in 1959 by J. P. H. Acocks, *Moraea amissa* was overlooked for some time, or only examined superficially. It was discovered some 10 km northwest of Malmesbury in an area of sandstone outcrops, now partly under cultivation. A search for this species by me in 1974 proved fruitless, and it is feared that this obviously rare plant may be extinct.

Surprising as it is to find an undescribed species from the Malmesbury district, a very well collected area, there can be no doubt that *M. amissa* is distinct from its suggested allies, *M. incurva* and *M. unguiculata*. Its very broad outer tepals are reminiscent of *M. villosa* though the flower is much smaller. The inner tepals are either entire or imperfectly tricuspidate and thus seem rather like those of *M. incurva*. This similarity is, however, superficial, and *M. amissa* is placed in section *Vieusseuxia* among the so-called "peacock moraeas," where the small flower, glabrous stem and leaf, and peculiar inner tepals distinguish it.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): 10 km NW of Malmesbury (BC), *Acocks 20739* (PRE).

51. **Moraea villosa** (Ker) Ker, Ann. Bot. (König & Sims) 1: 240. 1805.—FIG. 34E–F.

Iris villosa Ker, Bot. Mag. *tab. 571*. 1802. TYPE: Illustration in Bot. Mag. *tab. 571*.
Vieusseuxia villosa (Ker) Spreng., Syst. Veg. 1: 165. 1825.
Moraea pavonia (L.f.) Ker var. *villosa* (Ker) Baker, Fl. Cap. 6: 24. 1896.
Vieusseuxia aristata sensu Houtt., Handleid. 12: 105, *tab. 80*. 1780.

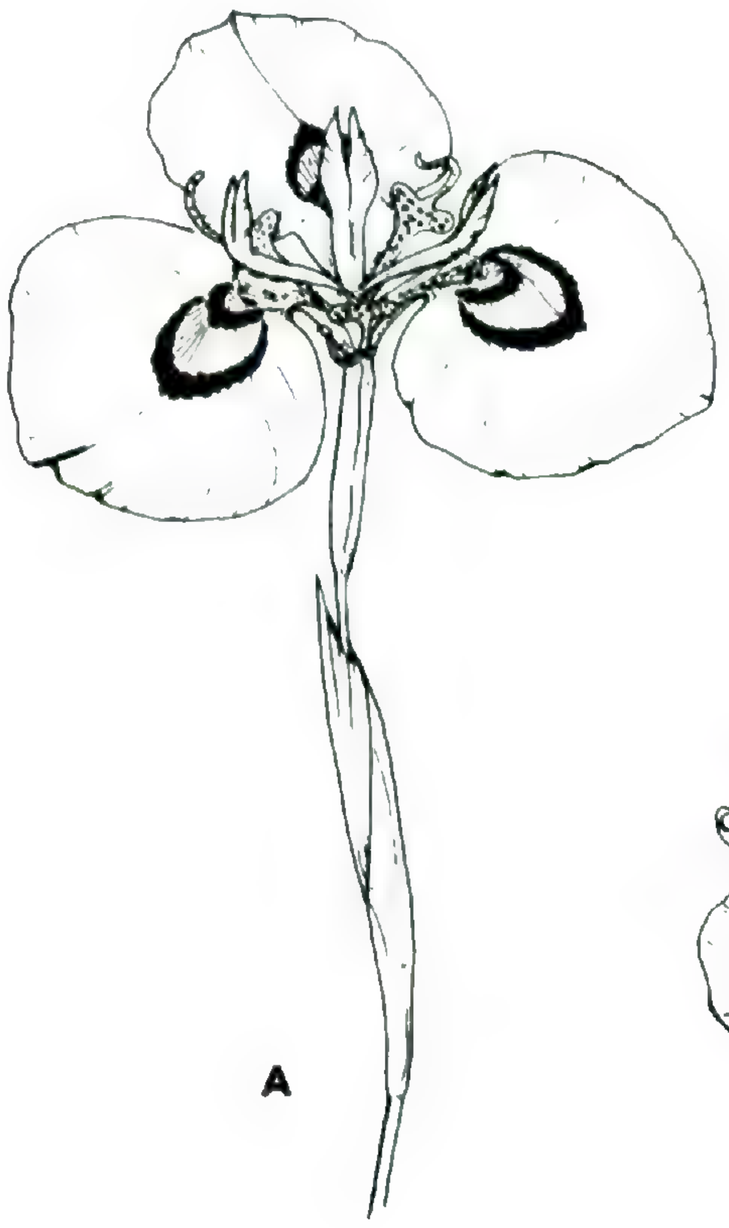
Plants (15–)20–40 cm high, often branched. *Corm* 1–1.5 cm in diameter; tunics of finely fibrous inner layers and coarse, almost woody, outer layers. *Leaf* solitary, linear, basal, usually pubescent on the outer surface, occasionally on the margins only, or rarely glabrous, exceeding the inflorescence. *Stem* villous, simple or 1–2-branched. *Spathes* herbaceous or dry above with brown, attenuate apices; inner spathe 4–6 cm long, the outer 2.5–4 cm long. *Flowers* various shades of purple, lilac, pink or occasionally cream to pale green with a prominent yellow nectar guide circled by a dark, contrasting color; outer tepals 3–4 cm long, the claw 0.8–1.2 cm, erect, the limb 2–2.5 cm wide, spreading; inner tepals 1.6–3.0 cm long, tricuspidate with 2 short lateral lobes, and a long ± spreading central acute cusp. *Filaments* ca. 5 mm long, free near the apex only; *anthers* 6–10 mm long, reaching the stigma or occasionally slightly exceeding it. *Style branches* 5–7 mm long, to 8 mm wide, the crests (2.5–)5–8 mm long, either well developed or fairly inconspicuous. *Capsule* cylindrical, 2–3 cm long; *seeds* angled with a spongy testa. Chromosome number $2n = 24$.

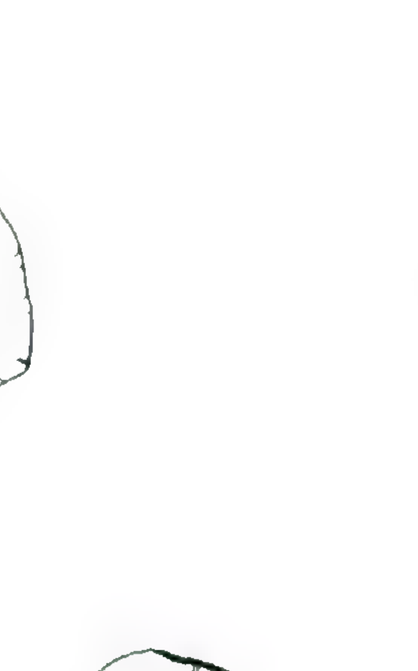
Flowering time: August to September.

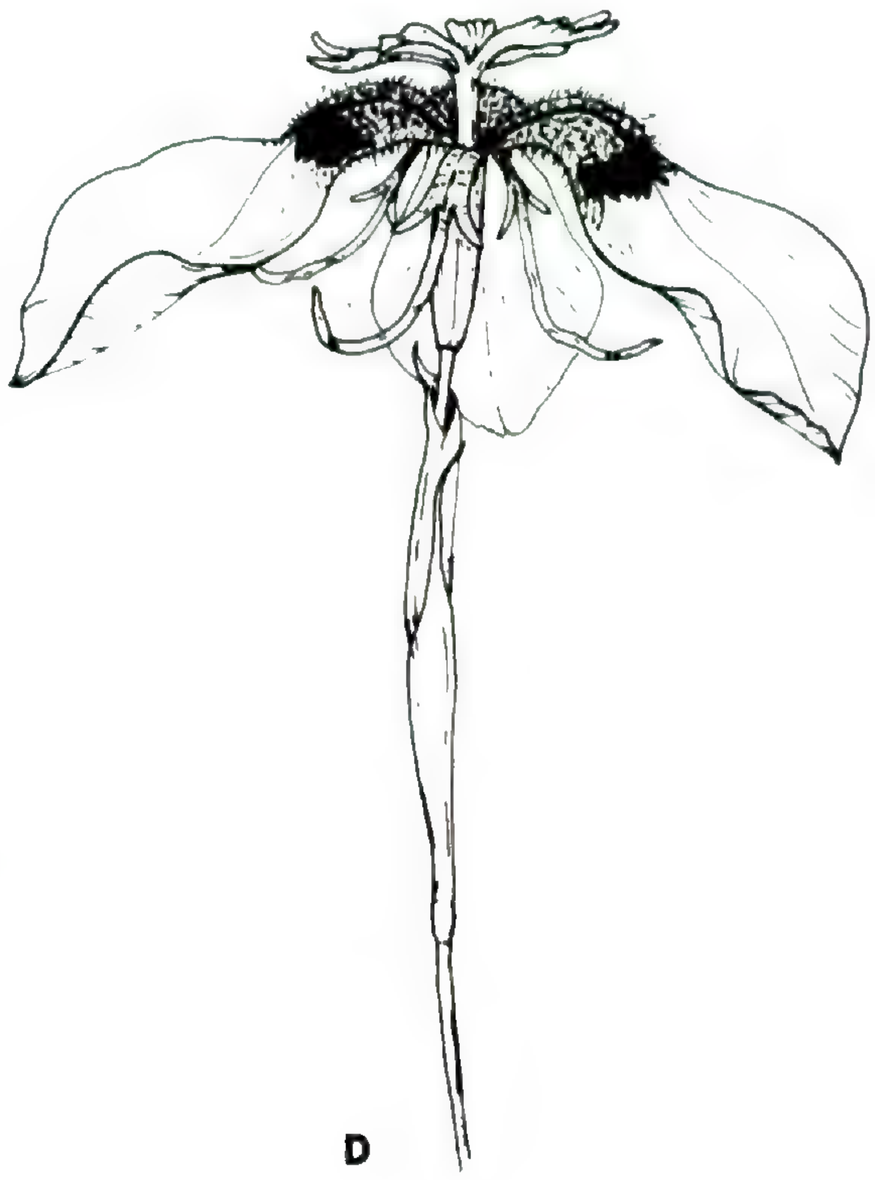
Distribution: Western Cape between Olifants River Valley and Hottentots Holland, usually on clay soils.—FIG. 34.

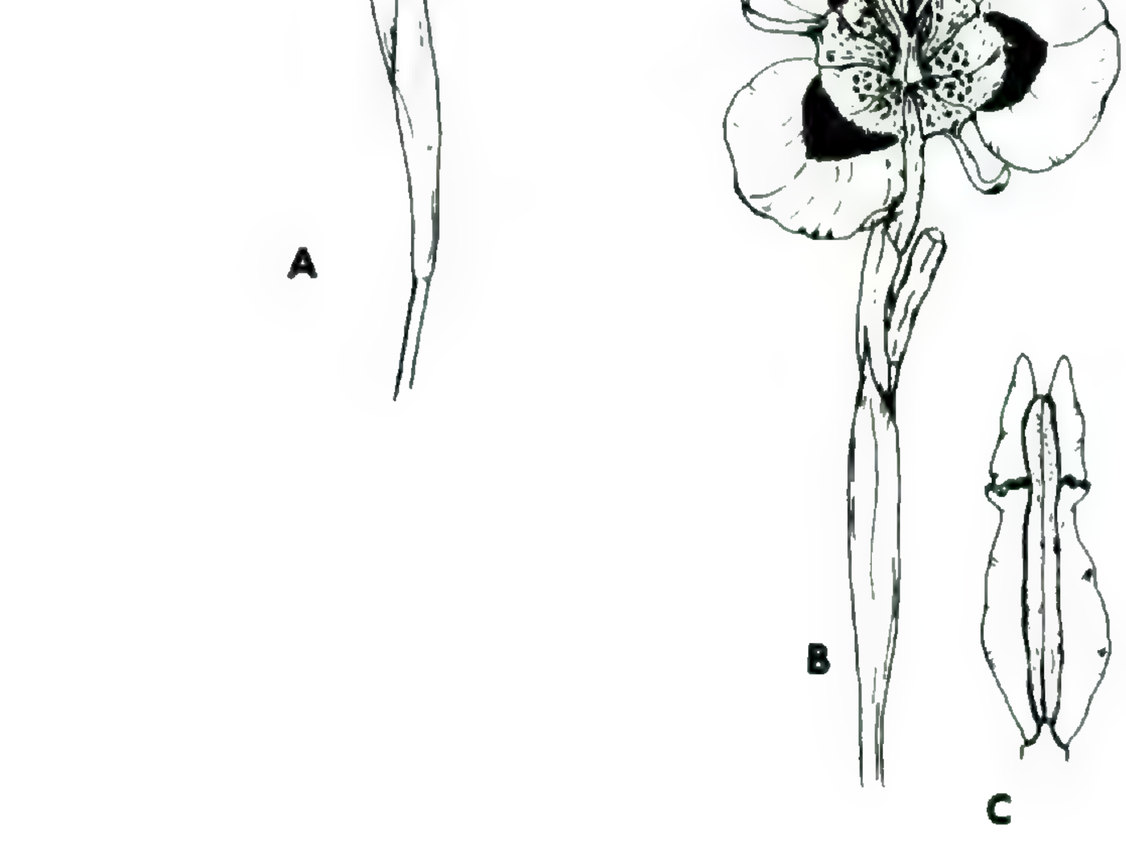
Moraea villosa was probably known in Europe for as long as were *M. aristata* and *M. neopavonia*, though it was not initially recognized as distinct. It was almost certainly first recorded by Thunberg, who accorded it varietal status as *Iris tricuspis* var. *purpurea*. Ker was the first to recognize it as a separate species in 1803, and after initially assigning it to *Iris*, he transferred it to *Moraea* in 1805.

It is the most widespread of all the "peacock moraeas," occurring along the









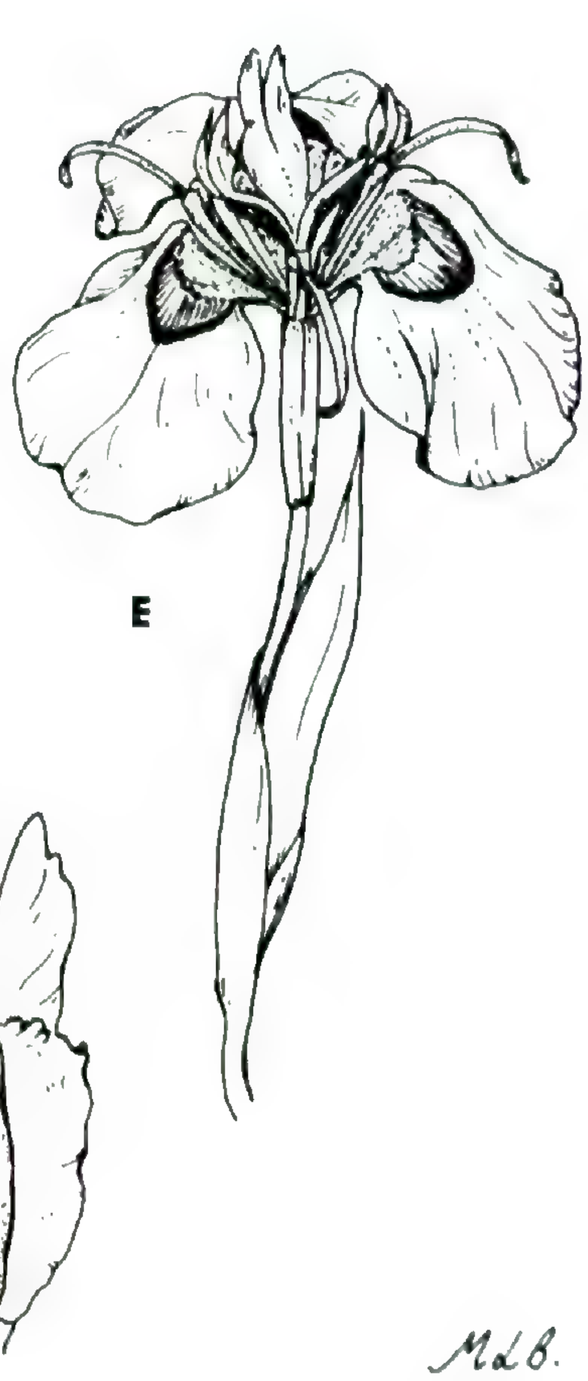


FIGURE 34. Distribution and floral morphology of "peacock moraeas."—A. *M. aristata*. Flower (life size).—B–C. *M. tulbaghensis*.—B. Flower (life size).—C. Style branch and anther (×3).—D. *M. loubseri*. Flower (life size).—E–F. *M. villosa*.—E. Flower (life size)—F. Style branch and anther (×3).

western Cape coastal belt from the Olifants River Valley, south to Sir Lowrys Pass, and it is common in the Tulbagh and Ceres districts. All populations examined cytologically have been found to be tetraploid, $2n = 24$, and the species may well be of allotetraploid origin.

Moraea villosa is somewhat variable in flower color; many populations have purple flowers with a navy, green, and yellow nectar guide, while others, notably in the Ceres area, have white, cream, pink, or rose flowers with contrasting markings, as well as the more usual purple color. The invariably pubescent stem and usually villous leaf, when taken together with flower color and size, are quite characteristic and distinguish *M. villosa* from its close allies, the glabrous *M. aristata*, and smaller, orange-flowered *M. tulbaghensis*.

SOUTH AFRICA. CAPE: 32.18 (Clanwilliam): Burgher's farm, Redelinghuys road (DC), *Barnard 266* (BOL). Foot of Piketberg, NE end (DD), *Pillans 7677* (BOL). Near Piketberg, *H. Bolus 13654* (PRE). Renosterkop, Piketberg, *Marloth 11538* (PRE).

32.19 (Wuppertal): 8 km N of Citrusdal (CA), *Lewis 5200* (NBG). Grootfontein road, Olifants River Mts. (CC), *Oliver 3966* (K, STE).

33.18 (Cape Town): Near Darling (AD), *H. Bolus 12835* (BOL). Near Porterville (BB), *Middlemost 1861* (BOL, NBG). Near Malmesbury (BC), *Lewis 1859* (SAM); *Barker 8050* (NBG). Near Agter Paarl (DB), *Reid sub Acocks 4918* (S). Paardeberg, *Salter 7667* (SAM). Wellington, *Lewis Grant 2390* (BR, M, MO). Fields near Durbanville (DC), *Esterhuysen 17511* (BOL). Near Klapmuts (DD), *Acocks 2169* (S).

33.19 (Worcester): Near Tulbagh (AC), *Garside 1537* (K); *Lewis Grant 2480* (BOL, BR, MO, PRE). Gouda, *Andrag s.n.* (STE-18578); (as Piketberg Road), *Guthrie s.n.* (NBG). Gydouw (AD), *Leipoldt 3007, 4079* (both BOL). Near Ceres, *H. Bolus 7340* (BOL); *Johnson 491* (NBG); Prince Alfreds Hamlet, *Lewis 2673* (SAM).

34.19 (Simonstown): Somerset West (BB), *Compton 13470* (NBG); *Leighton 248* (BOL). Near Gordons Bay, *H. Bolus s.n.* (BOL). Hottentots Holland, *Zeyher s.n.* (SAM-20600); *H. Bolus 6922* (BOL).

52. **Moraea tulbaghensis** L. Bol., S. African Gard. 22: 276. TYPE: South Africa, Cape, Saron, Tulbagh district, *L. Bolus s.n.* (BOL-16738).—FIG. 34B–C.

Plants 25–35 cm high, occasionally branched. *Corm* 1–1.5 cm in diameter; tunics of coarse, woody fibers. *Leaf* solitary, linear, basal, pubescent on the outer surface, usually exceeding the inflorescence. *Stem* villous, simple or 1-branched. *Spathes* herbaceous to dry above with dark attenuate apices; inner spathe 5–7 cm long, the outer ca. half the inner. *Flowers* much like *M. villosa* but bright orange, the nectar guide orange yellow, ringed with blue green; outer tepals ca. 2.4 cm long, the orange claw ca. 1 cm long, erect, bearded, the limb spreading, broad, to 2 cm wide; inner tepals 1.5–1.8 cm long, tricuspidate with 2 short lateral lobes and a long central ± spreading central cusp. *Filaments* ca. 5 mm long, free near the apex only; *anthers* 7–10 mm long, shortly exceeding the stigma lobes. *Style branches* ca. 7 mm long, to 3 mm wide, the crests triangular, ca. 2 mm long, inconspicuous. *Capsule* cylindrical, ca. 2 cm long; *seeds* large, angular, with a spongy testa. Chromosome number $2n = 24$.

Flowering time: September.

Distribution: Clay flats in the Tulbagh and Wellington districts of the southwestern Cape.—FIG. 34.

The brilliant orange-flowered *Moraea tulbaghensis* with its deep green and yellow nectar guide is morphologically very similar to *M. villosa*, and, except for

color differences, the two can be distinguished only with difficulty. *Moraea tulbaghensis* has, in general, slightly smaller flowers and particularly short style crests, ca. 2 mm long, in contrast with a range from 3 to 6 mm in *M. villosa*. Many collections of *M. tulbaghensis* also have anthers which exceed the stigmas, and this feature, as well as the orange flower color, is reminiscent of *M. neopavonia*. The distinctly tricuspidate inner tepals of *M. tulbaghensis* serve to distinguish it from this species.

Like *M. villosa*, *M. tulbaghensis* is evidently a polyploid species. In view of the morphological similarities an allotetraploid origin seems likely, with parent species similar to *M. neopavonia* and a diploid species resembling *M. villosa*, such as *M. aristata* or possibly *M. caeca*.

Moraea tulbaghensis occurs locally in the Tulbagh area, both in the Tulbagh valley and to the west, between Gouda and Saron. It is rare, and because it flowers irregularly, it is not often collected.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Twenty Four Rivers near Gouda (BB), *Leighton s.n.* (BOL). Roadside outside Wellington (DB), *Reid sub Acocks 4917* (S).

33.19 (Worcester): Saron (AA), *L. Bolus s.n.* (BOL-16738); *Andrag s.n.* (STE-18877). Near Gouda (AC), *Leipoldt s.n.* (BOL-20766). Mts. near Tulbagh Kloof, *Stokoe s.n.* (SAM-63679). Roadside in clay soil, Tulbagh, *Cheeseman sub Acocks 4922* (S). Near Tulbagh, *Ecklon & Zeyher Irid. no. 39* (SAM, LD); *Lewis Grant 2472* (BOL, K, MO).

Locality unknown: Ex hort. Kirstenbosch, *Meterlerkamp s.n.* (BOL).

53. **Moraea loubseri** Goldbl., Fl. Pl. Africa 42: *tab. 1724*. 1977. TYPE: South Africa, Cape, Olifants Kop, Langebaan, *Goldblatt 2076* (MO, holotype; K, NBG, PRE, S, isotypes).—FIG. 34D.

Plants 15–20 cm high, usually 1-branched. *Corm* ca. 1 cm in diameter; tunics of pale, fairly coarse fibers. *Leaf* solitary, basal, linear, pubescent, usually exceeding the inflorescence. *Stem* minutely pubescent, usually bearing a single branch. *Spathes* herbaceous with brown attenuate apices; inner spathe 4–5 cm long, the outer 3–4 cm long. *Flowers* blue violet with black pubescent centers; outer tepals ca. 2.3 cm long, the claw broad, ca. 1 cm long, completely bearded with black hairs, the limb slightly reflexed, 1.4–2 cm at the widest point; inner tepals 1.5–2 cm long, acuminate, tricuspidate, with 2 short lateral lobes and a long, ± spreading to slightly reflexed central cusp. *Filaments* ca. 4 mm long, free in the upper third; *anthers* 5 mm long. *Style branches* ca. 6 mm long, the crests ca. 1 mm, triangular. *Capsule* and *seeds* unknown.

Flowering time: Late August to September.

Distribution: Sandy soil on the summit of Olifants Kop, Langebaan, southwestern Cape.—FIG. 34.

Moraea loubseri is yet another extremely localized southwestern Cape species, being known only from a single small hill, Olifants Kop, near Langebaan in the Saldanha Bay area. Most remarkably, it was first discovered as recently as 1973, when Olifants Kop was visited by amateur botanists just before quarrying was scheduled to begin at this site (Goldblatt, 1977). The hill has subsequently been partially excavated and it seems only a matter of time before the natural habitat of *M. loubseri* is entirely destroyed. Fortunately, authorities have been

alerted to the situation and a small nature reserve may be set aside to preserve this plant. It has also been introduced to horticulture, and because of its beauty and relative ease of cultivation, it may become an established garden favorite.

The species is clearly allied to the "peacock" group, particularly *Moraea villosa* which it resembles in the pubescence of stem and leaf and in flower size. The blue color and remarkable black beard covering the claw and proximal part of the limb of the outer tepals is, however, so distinctive that confusion with any other species seems unlikely.

SOUTH AFRICA. CAPE: 33.18 (Cape Town): Olifants Kop near Langebaan (AA), *Goldblatt 2706* (K, MO, NBG, PRE, S); *Loubser 2228* (NBG).

V. Subgenus GRANDIFLORA

Subgenus **Grandiflora** Goldbl., Ann. Missouri Bot. Gard. 63: 8. 1976. TYPE: *Moraea spathulata* (L.f.) Klatt.

Plants medium to large, rarely branched. *Corm* tunics usually pale to brown and fibrous. *Prophylls* often distinctive, large, entire to fibrous, or irregularly broken, dark brown to pale. *Leaf* solitary, flat, canaliculate or revolute. *Flowers* usually large, usually yellow or white, blue purple in a few species; outer tepals spreading; inner tepals entire, and usually erect. *Style branches* and crests well developed. *Capsule* clavate-cylindrical; *seeds* large, flattened and triangular to discoid. Basic chromosome number, $x = 6$.

Distribution: Extending from the southern Cape through southern and tropical Africa to Ethiopia and Nigeria, found mainly in highland areas.

This subgenus, comprising about 22 species occurs mainly in regions of summer rainfall and is found throughout sub-Saharan Africa in highland areas. There is a remarkable degree of morphological uniformity in the group, all species having a very similar flower and vegetative form. Species have, however, become adapted to a variety of habitats and ecological niches and in this respect exhibit greater diversity than other subgenera of *Moraea*.

The basic chromosome number $x = 6$ is clearly specialized, which accords with the considerable specialization of the subgenus where the leaf is invariably solitary and the stem unbranched, except in the rarest of cases. The flowers are, however, quite typical for the genus, except in being large, but the flattened seeds are clearly specialized. Though subgenus *Grandiflora* shares the same basic chromosome number, $x = 6$, with subgenus *Vieusseuxia*, there is no reason to believe that they are related or have a common origin. As the two subgenera have become specialized in quite different ways, they are perhaps more likely to have evolved independently of one another.

54. **Moraea spathulata** (L.f.) Klatt.

This species occurs throughout the eastern mountains of South Africa, and extends along the coast southwards to the George district of the southern Cape. It is thus predominantly a summer-rainfall-area species, and as such was dealt with in detail in the treatment of *Moraea* for this area (Goldblatt, 1973: 250).

The type was collected by Thunberg in the southern part of its range, and only the typical subspecies occurs in the winter rainfall area.

EXCLUDED SPECIES

Of the many species of *Moraea* from the southern African winter rainfall region now regarded as belonging to other genera, only the following remain unidentified or have not already been placed in other genera.

Moraea capensis (Burm. f.) Klatt, Durand & Schinz, Consp. Fl. Afr. 5: 148. 1895.

This species was first described by Burman fil. as *Iris capensis*. The type specimen, in the Burman Herbarium, in the Delessert Herbarium, Geneva shows it to be *Iris xiphium* L., evidently in cultivation at the Cape in the eighteenth century.

Moraea crispa Thunb., Diss. de Moraea 13. 1787.

The identity of this species, collected by Thunberg, and still represented in his herbarium at Uppsala, remains a mystery. The species is clearly unifoliate, with a crisped and undulate basal leaf, and has an unbranched stem. Beyond the fact that the flowers were blue, nothing is known. The species is either a *Homeria* or a *Moraea*, but no plant is known in either genus with such leaf characters from the Roggeveld where the original gathering was made. This area is not particularly well collected, and plants matching the Thunberg collection may eventually be found so that the true identity of *M. crispa* can be established.

Moraea gigantea Klatt, Linnaea 35: 381. 1868.

This is a species of *Homeria* and will be assigned to this genus when my planned revision of *Homeria* is completed.

Moraea gracilis (Licht. ex R. & S.) Dietr., Sp. Pl., ed. 6, 1: 478. 1833.

Type material of this species, based on *Iris gracilis* Licht. ex R. & S., has not been located and in its absence must be excluded. The description of *Iris gracilis*, a plant collected by Lichtenstein on the Cape Peninsula, alone is not sufficient for determination.

Moraea juncea L., Sp. Pl., ed. 2: 59. 1762.

Known only from the brief Linnaean diagnosis, this species remains something of a mystery (Barnard & Goldblatt, 1975). As it cannot be identified with any known species or specimen, it must be excluded (see p. 693).

Moraea fasciculata Klatt, Abh. Naturf. Ges. Halle 15: 367.

Klatt intended this name for a form of what is here recognized as *M. falcifolia* Klatt. However, in citing *M. largiflora* Ker as a synonym, Klatt in effect makes

the species superfluous. *Moraea largiflora* Ker does not exist, but is possibly a misspelling of *M. longiflora.*

Moraea minuta (L.f.) Ker, Ann. Bot. (König & Sims) 1: 241. 1805.

Based on *Iris minuta* L.f. and typified by specimens in the Thunberg Herbarium, *M. minuta* is readily identified as either *M. ciliata* or what is recognized here as *M. tricolor* Andr. Flowers of the type are preserved too poorly to pick out critical differences, and the descriptions given by Thunberg of both *Iris ciliata* and *I. minuta* are confusing. Both are reputed to have come from the Cape Peninsula, where *M. tricolor* is not recorded, and to have had yellow flowers, yet the only population of *M. ciliata* known to me in the area is blue flowered. *Iris minuta* is described as being glabrous, a characteristic of *M. tricolor*, but with narrow inner tepals, a feature of *M. ciliata.* The confusion cannot be resolved with the information presently at hand and the species must thus be rejected.

Moraea pritzeliana Diels, Bot. Jahrb. Syst. 44: 117. 1910.

Examination of the type at the Botanical Museum at Berlin-Dahlem shows this to be conspecific with *Gynandriris torta* (L. Bol.) Foster. As it is an earlier synonym, the following new combination is necessary:

Gynandriris pritzeliana (Diels) Goldbl., comb. nov.

Moraea pritzeliana Diels, Bot. Jahrb. Syst. 44: 117. 1910. TYPE: South Africa, Cape, Calvina district, *Diels 694* (B, holotype).
Moraea torta L. Bol., S. African Gard. 17: 418. 1927.
Gynandriris torta (L. Bol.) Foster, Contr. Gray Herb. 114: 41. 1936.

Moraea zeyheri Lehm., Ann. Sci. Nat. Bot., sér. 2, 6: 107. 1836.

The type specimen of this species, described by Lehman, has not been located, and in its absence identification of this species is not possible.

Literature Cited

Acocks, J. P. H. 1953. Veld Types of South Africa. S. African Dep. Agric. Bot. Surv. Mem. 28. Government Printer, Pretoria.

Adamson, R. S. 1938. The Vegetation of South Africa. British Empire Vegetation Committee, London.

Arber, A. 1921. The leaf structure of the Iridaceae considered in relation to the phyllode theory. Ann. Bot. 35: 301–336.

Axelrod, D. I. 1973. History of the Mediterranean ecosystem in California. Pp. 225–277, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems—Origin and Structure. Springer-Verlag, New York.

Baker, J. G. 1892. Handbook of the Iridaceae. G. Bell & Sons, London.

———. 1896. Irideae. *In* W. T. Thiselton-Dyer (editor), Flora Capensis. Vol. 6: 7–71. Reeve & Co., Ashford, Kent.

———. 1898. Irideae. *In* W. T. Thiselton-Dyer (editor). Flora of Tropical Africa. Vol. 7: 337–376. Reeve & Co., London.

Barnard, K. H. 1947. A description of the Codex Witsenii in the South African Museum. J. S. African Bot. 13: 1–52.

Barnard, T. T. & P. Goldblatt. 1975. A reappraisal of the application of specific epithets of the type species of *Moraea* and *Dietes* (Iridaceae). Taxon 24: 125–131.

Breyne, J. 1739. Prodromus Fasciculi Rariorum Plantarum . . . . Schreiber, Danzig.

BROWN, N. E. 1928. The Iridaceae of Thunberg's Herbarium. J. Linn. Soc. Bot. 48: 34–42.
———. 1929. Contributions to a knowledge of the Transvaal Iridaceae. Trans. Roy. Soc. S. Africa 17: 341–352.
BURMAN, J. 1738–1739. Rariorum Africanarum Plantarum. Boussiere, Amsterdam.
DAHLGREN, R. 1963. Studies on *Aspalathus*. Phytogeographical aspects. Bot. Not. 116: 431–472.
———. 1968. Distribution and substrate in the South African genus *Aspalathus* L. (Leguminosae). Bot. Not. 121: 505–534.
EDWARDS, D. & O. A. LEISTNER. 1971. A degree reference system for citing biological records in Southern Africa. Mitt. Bot. Staatssamml. München 10: 501–509.
FOSTER, R. C. 1939. Studies in the Iridaceae I. Contr. Gray Herb. 127: 33–48.
GOLDBLATT, P. 1971. Cytological and morphological studies in the southern African Iridaceae. J. S. African Bot. 37: 317–460.
———. 1972a. A revision of the genera *Lapeirousia* Pourret and *Anomatheca* Ker in the winter rainfall region of South Africa. Contr. Bolus Herb. 4: 1–111.
———. 1972b. *Moraea insolens* Goldbl. Fl. Pl. Africa 42: *tab. 1639*.
———. 1973. Contribution to the knowledge of *Moraea* (Iridaceae) in the summer rainfall region of South Africa. Ann. Missouri Bot. Gard. 60: 204–259.
———. 1976a. Evolution, cytology and subgeneric classification in *Moraea* (Iridaceae). Ann. Missouri Bot. Gard. 63: 1–23.
———. 1976b. *Barnardiella*: a new genus of the Iridaceae and its relationship to *Gynandriris* and *Moraea*. Ann. Missouri Bot. Gard. 63: 309–313.
———. 1977. *Moraea loubseri* Goldbl. sp. nov. Fl. Pl. Africa 42: *tab. 1724*.
——— & T. T. BARNARD. 1970. The Iridaceae of Daniel de la Roche. J. S. African Bot. 36: 291–318.
GOOD, R. 1968. The Geography of the Flowering Plants. Ed. 3. Longmans, London.
HOUTTYN, M. 1780. Naturrliike Historie. Ser. 2. Vol. 12. Erven van F. Houttuyn, Amsterdam.
JACQUIN, N. 1776. Hortus Botanicus Vindobonensis. Vol. 3. Kaliwoda, Vienna.
JESSOP, J. P. 1966. A volume of early water-colours in the library of the Botanical Research Institute, Pretoria. J. S. African Biol. Soc. 6: 38–52.
KER, J. B. 1803. *Moraea edulis*. Long-leaved *Moraea*. Bot. Mag. 17: *tab. 613*.
——— (as Gawler, J. B.). 1805. Ensatorum ordo. Ann. Bot. (König & Sims) 1: 219–247.
———. 1827. Iridearum Generum. De Mat, Brussels.
LEWIS, G. J. 1948. *In* W. F. Barker, J. J. Lewis, M. R. Levyns & C. E. Moss. Plantae Novae Africanae. J. S. African Bot. 14: 29–40.
———. 1949. *Moraea angusta* (Thunb.) Ker and allied species. J. S. African Bot. 15: 116–120.
———. 1954. Some aspects of the morphology, phylogeny and taxonomy of the South African Iridaceae. Ann. S. African Mus. 40: 15–113.
LINNAEUS, C. 1762. Species Plantarum. Ed. 2. Salvius, Stockholm.
LINNAEUS, C. VON, FILIUS. 1781. Supplementum Plantarum. Orphanotropheus, Braunschweig.
MACNAE, M. M. & L. E. DAVIDSON. 1969. The volume "Icones Plantarum et Animalium" in the African Museum, Johannesburg and its relationship to the Codex Witsenii quoted by Jan Burman in his "Decades Rariorum Africanum Plantarum." J. S. African Bot. 35: 65–82.
NORDENSTAM, B. 1969. Phytogeography of the genus *Euryops* (Compositae). Opera Bot. 23: 1–77.
RAVEN, P. H. 1964. Catastrophic selection and edaphic endemism. Evolution 18: 336–338.
———. 1973. The evolution of Mediterranean Floras. Pp. 213–224, *in* F. di Castri & H. A. Mooney (editors), Mediterranean Type Ecosystems—Origin and Structure. Springer-Verlag, New York.
SALISBURY, R. A. 1812. On the cultivation of rare plants such as have been introduced since the death of Mr. Philip Miller. Trans. Hort. Soc. London 1: 261–366.
SCOTT-ELLIOT, G. F. 1891. Notes on the fertilization of South African and Madagascar flowering plants. Ann. Bot. 5: 333–405.
SPAE, D. 1846. *Dietes bicolor*. Ann. Soc. Roy. Agric. Gand. 2: 233–234.
SWEET, R. 1830. Hortus Britannicus. Ed. 2. Ridgeway, London.
WEIMARCK, H. 1941. Phytogeographical group, centres and intervals within the Cape Flora. Acta Univ. Lund., n.s., 37: 5–143.

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Numbers in **boldface** refer to descriptions; names in roman are recognized as valid; names in *italic* refer to synonyms and illegitimate names; numbers with asterisks (*) refer to names incidentally mentioned.

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aristata sensu Houtt. 775
aurantiaca Eckl. & Zey. 764*
bellendenii Sweet 767

bituminosa (L.f.) Eckl. 732
brehmii Eckl. 689
edulis (L.f.) Link. 725
freuchenia (Eckl.) Steud. 687
fugax de la Roche 725, 773
geniculata Eckl. 706
glaucopis DC. 773, 774*
graminifolia Eckl. 693
intermedia Eckl. 699
lurida (Ker) Sweet 762
mutila C.H. Berg ex Eckl. 751
nervosa Eckl. 699
pavonia (L.f.) DC. 769, 774*
pulchra Eckl. 751
rivularis Eckl. 693
spiralis de la Roche 676*, 681, 745, 749, 767, 768*
tenuis (Ker) R. & S. 759
tricuspis (Thunb.) Ker 765
tripetala (L.f.) Klatt 751
tripetaloides DC. 751
villosa (Ker) Spreng. 775
viscaria (L.f.) Eckl. 735

STUDIES IN NEOTROPICAL PALEOBOTANY. II. THE MIOCENE COMMUNITIES OF VERACRUZ, MEXICO[1, 2]

ALAN GRAHAM[3]

ABSTRACT

Lignites containing a diverse and well-preserved pollen and spore flora were obtained from the upper Miocene Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico. Among modern communities reflected in the fossil microflora are Needle-Leaved Forests of bosque de oyamel, bosque de pino, and bosque de pino y encino; Broad-Leaved Forests of warm, temperate and evergreen oak communities; Deciduous Forest; Temperate and Saline Grasslands; Mangrove Swamps; Coastal Dune Vegetation; a restricted and modified Low Deciduous Selva; and possibly Paramo, Inland Swamp, and Aquatic Vegetation. Absent or poorly represented are the Scale-Leaved Forests of bosque de cedro y táscate; High Evergreen Selva (tropical rain forest); High Semi-Evergreen Selva; Medium Semi-Evergreen Selva; Low Evergreen Selva; Low Semi-Evergreen Selva; Low Thorn Selva; Palm Stands; Savannas; *Nolina-*

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[1] Research for this study was supported by NSF grants GB-5671 and GB-11862.

[2] These investigations on the Cenozoic history of Mexican vegetation began in 1965, and during the period of study many individuals have provided assistance that is greatly appreciated. Dr. J. Rzedowski, Instituto Politécnico, made arrangements through Dr. Cortez Obregon for cooperation of the Consejo de Recursos Naturales No Renovables. Dr. Cortez Obregon supplied coal and lignite samples from several localities in Mexico, and Dr. Rzedowski has continued to provide very helpful information on Mexican vegetation.

In 1967 Dr. Arturo Gómez-Pompa arranged discussions with Dr. Agustín Ayala-Castañares and Ing. Guillermo P. Salas, Instituto Geología, UNAM, concerning various facets of Mexican geology. As a result of these discussions, samples were eventually obtained from Coatzacoalcos, Veracruz through the offices of the Petróleos Mexicanos and Ing. Roberto Gutierrez Gil, Superintendente, Zona Sur. Subsequently other geological information was provided by Dr. Jaime Rueda-Gaxiola, Instituto Mexicano del Petróleo. During the 1967 field season Dr. David Jarzen and Dr. Enrique Martínez-Hernández capably assisted in the collection of samples.

Interpretation of the palynological data has been facilitated by numerous conversations with members of the Departamento de Botánica, UNAM, including Drs. Ramon Riba, José Sarukhán, Mario Sousa, and Dr. Arturo Gómez-Pompa. In addition to providing valuable suggestions on the distribution and ecological significance of taxa identified from the Paraje Solo microflora, Dr. Gómez-Pompa organized a visit to Veracruz in 1971 for study of various community types represented in the fossil assemblage.

Of particular importance to this study are data and publications resulting from the Flora Veracruz Project (see Gómez-Pompa & Nevling, 1970). As a guide for processing relevant pollen and spore reference material and for distribution information, it is necessary to know the composition of the regional vegetation. In previous studies on Latin American paleobotany accumulating this information from herbarium sheets has been a lengthy and tedious task. As part of the Flora Veracruz Project a computer program has been designed, and this facet of the project has been of inestimable value for our studies on the vegetational history of Veracruz. Rather than the 2–3 months required to accumulate a list of important plants in the modern flora, a print-out of 6,049 species names was generated in less than 30 minutes. The completion of the Flora Veracruz will be an important contribution to the botany of Latin America, and in the meantime general summaries of the vegetation and soils (Gómez-Pompa, 1973), climates (García, 1970), and the developing retrieval system are most appreciated by those of us dependent on information about the modern communities.

A number of individuals provided helpful information on specific points of the study, including especially Drs. Dennis Breedlove, Michael D. Coe, Paul Colinvaux, Margaret Davis, E. S. Deevey, Richard A. Howard, Daniel Livingstone, Rogers McVaugh, Lorin Nevling, Reinhard Weber, and H. E. Wright.

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Hechtia-Agave Desert; and Thorn Scrub. The presence of pollen of *Picea* in the microflora suggests cooler temperatures during the upper Miocene and possibly greater and more uniformly distributed rainfall. This type of paleoenvironment would account for the poor representation of both the tropical rain forest and communities of arid aspect, and account for the prominence of the temperate Deciduous Forest in the upper Miocene paleocommunities.

The region of southern Veracruz is biologically one of the most interesting in northern Latin America. Because of its location at a transition between tropical and temperate environments, with topographic diversity ranging from sea level to the highest altitudes in Mexico, an array of vegetation types and considerable species diversity characterizes the flora. The lowlands contain remnants of a tropical rain forest (Selva Alta Perennifolia) with floristic affinities primarily to the south, while the mid-altitude eastern slopes of the Sierra Madre Oriental support an oak-*Liquidambar* deciduous forest (Bosque Caducifolio) containing some 60 species of arborescent plants also found in the temperate forests of the eastern United States. Historical factors have been important in the development of the biota since southeastern Veracruz is situated at the confluence of an Antillean-Central American migration route that has operated throughout the Cenozoic. With land surfaces gradually increasing in the Greater and Lesser Antilles during the Tertiary, and climatic fluctuations affecting the range of various neotropical species, numerous floral and faunal elements have converged on and radiated from the intersection of these two migration routes. The diversity in habitats, available since the initial uplift of the Sierra Madre Oriental beginning near the end of the Cretaceous, and continuing through the Cenozoic, allowed many of these elements to persist, creating a diverse flora estimated at some 10,000 species.

The region is also of interest as the site of one of the oldest sedentary agricultural populations in Latin America. The "Olmec Heartland" was being occupied and cultivated nearly 5,000 years ago, near the end of the climatic Xerothermic Period (ca. 8,000–4,000 B.P.), and several plant associations present today, but absent or poorly represented in the Miocene flora, may be attributable to the milpa farming practices of the Olmecs and subsequent civilizations introduced near the end of a prolonged dry period (e.g., savannas, palm stands of *Scheelea* and *Sabal*, and certain communities of dry aspect).

The Veracruz studies were undertaken to provide a better understanding of the vegetation and its development during the Cenozoic. The preliminary results indicate, however, that rather than confirming earlier impressions, considerable revision is necessary in our concepts of the vegetation of the region. For example, the existing literature suggests that elements of the deciduous forest (*Acer*, *Juglans*, *Fagus*, *Liquidambar*, *Almus*, *Ulmus*, *Populus*, *Platanus*, *Cornus*, *Salix*, and others) are recent introductions corresponding to times of maximum glacial advance, while the tropical rain forest is an ancient community occupying lowland regions of stable unchanging environments. In fact, elements of the temperate deciduous forest were already well established in southeastern Mexico by the end of the Miocene, and evidence is accumulating that the modern tropical rain forest may be of Post-glacial origin of less than 11,000 years.

In evaluating the Veracruz data it should be noted that there are no other Miocene microfloras published for Latin America, and the only megafossil flora is that discussed by Berry (1923). Virtually nothing is known of pollen release and transport or pollination mechanisms for important neotropical genera represented by pollen in the fossil assemblage, and only recently has the present-day vegetation been adequately enough characterized (Gómez-Pompa, 1973) to allow comparison of the modern and Miocene communities. These difficulties impart a tentative aspect to interpretations that undoubtedly will be altered and refined in future studies. For the moment, however, the near absence of information on vegetational history for northern Latin America warrants presenting even these preliminary data on the upper Miocene flora of southeastern Veracruz.

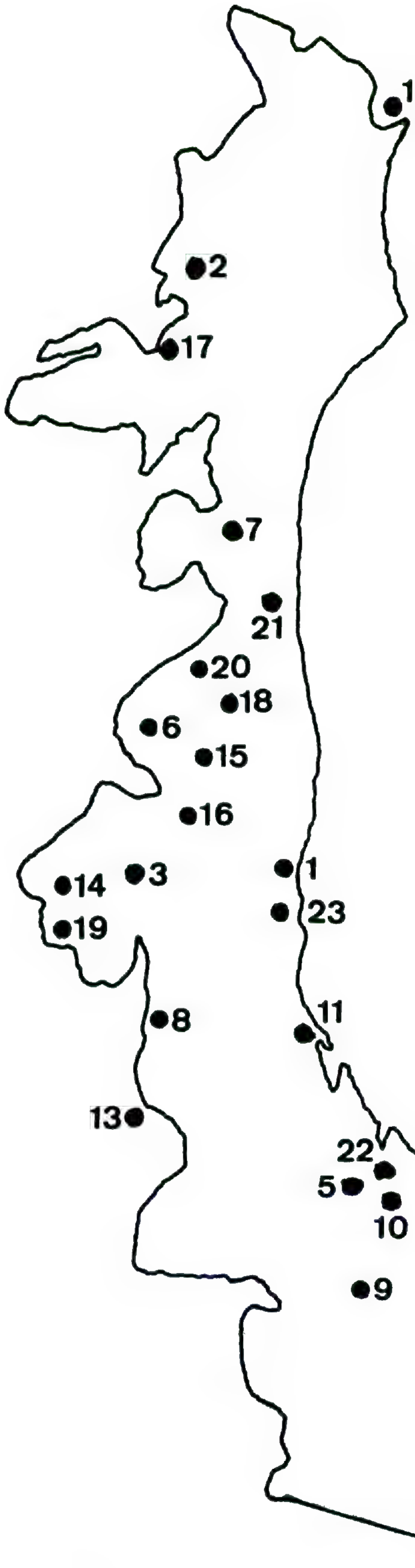
Physiography and Climate

Veracruz is the most physiographically diverse state of Mexico, extending through 5° latitude (17°10′ to 22°20′N; Fig. 1). The state is mostly flat, low-lying coastal plain of less than 300 m elevation. In west-central Veracruz, however, two important mountain systems converge, a branch of the Sierra Madre Oriental and an eastern extension of the Cinturon Neovolcánico (Transvolcanic Belt). These mountains include the highest peak in Mexico, Pico de Orizaba (5,747 m). The major period of uplift began during the Cretaceous as part of the "Laramide Revolution" that characterized the end of the Mesozoic Era. These highlands are located about 325 km NW of the collection localities at Coatzacoalcos.

Another mountainous area in Veracruz is the Sierra de los Tuxtlas to the south and inland from the coast, about 100 km NW of Coatzacoalcos. These mountains are of volcanic origin and the exposed basalts are of Miocene-Pliocene age (Salas, 1968). The highest elevation is about 1,700 m. Climates of the northernmost portion of the state are influenced by the Sierra de Tamaulipas, around the port of Veracruz by the Sierra de Chiconquiaco, and in the southernmost part of the state by branches of the Sierra Madre del Sur which reach about 1,000 m. The Sierra de Tantima consists of a few low mountains about 700 m in elevation near Tantoyuca (see Fig. 1 for place names).

As a consequence of its longitudinal extent and topographic diversity the range of climates in Veracruz is extensive (García, 1970). Near the summit of Pico de Orizaba average annual temperatures are below –2°C and frost occurs about 40 days per year. At intermediate elevations along the east and west slopes of the mountains, at elevations between about 500 and 2,000 m, extending (N–S) from Chicontepec through Papantla, Jalapa, Córdoba, to Tierra Blanca, is a temperate zone with average annual temperatures between 12 and 18°C. The greatest portion of Veracruz (the coastal plain below about 300 m elevation) is hot with average annual temperatures between 22 and 26°C. In the vicinity of Veracruz and in low-lying inland areas and valleys to the south annual temperatures average slightly above 26°C.

Rainfall in Veracruz is from about 500 mm annually to more than 4,000 mm. Regions of highest rainfall are in the south, along the coast in the vicinity of San Andrés de Tuxtla (ca. 4,000 mm) and along the western border of the state



1. Veracruz
2. Tantoyuca
3. Cordoba
4. Coatzacoalcos
5. S. A. de Tuxtla
6. Cofre de Perote
7. Papantla
8. Tierra Blanca
9. Acayucan
10. Volcan San Martin
11. Alvarado
12. Tampico
13. Tuxtepec
14. Orizaba
15. Jalapa
16. Huatusco
17. Chicontepec
18. Naolinco
19. Acultzingo
20. Tlacolulan
21. Colipa
22. Coyame
23. Mandinga

FIGURE 1. State of Veracruz, index map of place names.

around Tierra Blanca (3,500–4,000 mm). The driest areas are on the western slopes of the west-central mountainous zone, in the northernmost portion of the state, created by the Sierra de Tamaulipas; in the region inland from the port of Veracruz, created by the Sierra de Chiconquiaco; and on the west side of the Sierra de los Tuxtlas in the south-central portion of the state (800–1,200 mm annually). Depending on the distribution of rainfall, regions in Veracruz have uniform precipitation (with at least about 18% of the rain falling during the dry season of December through May) or summer rains (with less than about 18% falling during the dry season). The seasonal rainfall is controlled by the trade winds (bringing summer rains), but in some regions summer rains are supplemented by winter precipitation from polar air masses (nortes) to produce a more uniform yearly rainfall. The distribution of rainfall is a visibly important factor in determining the aspect and composition of vegetation in Veracruz. The occurrence of evergreen, semievergreen, and deciduous selvas is in part a reflection of the degree and extent of the dry winter season.

In low-lying coastal areas in the north (e.g., just south of Tampico), and at higher elevations inland (e.g., Jalapa, Acayucan) fog is common (80–100 days per year). In the latter region is the vegetation, occupying mid-altitude temperate zones along the eastern escarpment, commonly referred to as cloud forest.

In the immediate vicinity of the collecting localities at Coatzacoalcos the average annual temperature is between 22 and 26°C. The minimum temperature recorded during the past 50 years is 10°C. Rainfall is about 3,000 mm annually with winter rain accounting for about 10–18% of the total. The monthly distribution of rainfall is: January, 134 mm; February, 72; March, 57; April, 51; May, 112; June, 267; July, 233; August, 297; September, 500; October, 525; November, 282; December, 195. Other aspects of the climates of Veracruz have recently been summarized by Gómez-Pompa (1973).

Modern Vegetation

One of the most difficult aspects of vegetational history studies in tropical regions is sorting miscellaneous genera identified from fossil microfloras into communities corresponding, as far as possible, to modern associations. Information available on modern vegetation types and their distribution, composition, and ecological parameters is essential to the reconstruction of paleocommunities and paleoenvironmental interpretations. The initial phase of Studies in Neotropical Paleobotany concerns Mexico, Panama, and Puerto Rico partly because through several current research projects the vegetation of these countries is sufficiently well known to allow recognition and characterization of communities.

A survey of Mexican vegetation reveals some modern associations well represented in Veracruz during the upper Miocene, while other climatically and geographically distinct types are absent. In the following discussion genera marked with an asterisk (*) are represented by fossil pollen in the upper Miocene Paraje Solo Formation of Veracruz. Various pollen types of the stenopalynous Cyperaceae, Gramineae, Chenopodiaceae-Amaranthaceae, and Com-

positae could not be generically identified. Pollen of the large and important tropical plant family Lauraceae is destroyed by standard processing techniques and presumably does not fossilize.

GENERAL VEGETATION OF MEXICO

The modern vegetation of Mexico is known through floristic studies (Shreve & Wiggins, 1964, Sonora; Rzedowski, 1961, San Luis Potosí; Rzedowski & McVaugh, 1966, Nueva Galicia; Breedlove, 1973, Chiapas), monographs (Clausen, 1959, *Sedum*; Martínez, 1963, Pinaceae; Gentry, 1972, Agavaceae), and maps (Leopold, 1950). The most recent summary of Mexican vegetation is the map and accompanying text, *Tipos de Vegetación de la Republica Mexicana* (Flores Mata, et al., 1971), and the *Guias Botanicas de Excursiones en México* (Sociedad Botánica de México, 1972).

Following terminology used in the *Tipos de Vegetación*, the primary vegetation of Mexico is classified into 25 principal types.

Vegetación Hidrofila.—

(1). *Manglar*—Mangrove swamps of *Rhizophora* mangle* L., *Avicennia germinans* L., *Laguncularia* racemosa* (L.) Gaertn.f., and *Conocarpus erecta* L. In southeastern Mexico manglar vegetation is found along the coast and inland from Alvarado, and from Coatzacoalcos continuing around coastal Yucatán Peninsula.

(2). *Popal*—Herbaceous, fresh-water marsh vegetation characterized by plants with large, broad leaves and anchored in relatively deep water. Important genera are *Calathea, Thalia, Leersia, Paspalum, Panicum, Oryza, Zizaniopsis,* and *Hymenachne.* Popal vegetation occurs scattered along the southeastern coast (e.g., just southwest of Coatzacoalcos) and is especially well developed in an extensive area around Bahía Ascención, eastern coastal Yucatán.

(3). *Tular y Carrizal*—Reed-Sedge marshes of *Phragmites australis* (Cav.) Trin. ex Steud., *Scirpus californicus* (Meyer) Steud., *Cyperus giganteus* Vahl, and *Typha.* Sedge and reed marshes are locally developed around Largo Texcoco and in lowlands east of Toluca, and scattered throughout southestern Mexico.

(4). *Palmar*—Palm stands along the coast in warm to hot climates. The common genera include *Scheelea, Orbignya, Sabal, Pseudophoenix, Paurotis, Brahea,* Roystonea, Washingtonia.* In southeastern Mexico there are extensive palm stands inland from Alvarado, and smaller scattered communities around Coatzacoalcos, Villahermosa, and along the Río Usumacinta.

(5). *Sabana*—Savannas of *Byrsonima crassifolia* (L.) DC., *Curatella americana* L., *Crescentia alata* H.B.K., *C. cujete* L., and understory grasses of *Andropogon, Paspalum, Trichachne, Imperata, Trachypogon,* and *Manisuris.* Extensive savannas occur just to the north of Palenque and Pichucalco, and between Tuxtepec and San Andrés Tuxtla.

Selva.—Arborescent vegetation of warm tropical lowlands and generally with several to many common tree species (a "multidominant" community).

(6). *Alta Perennifolia* (High Evergreen Selva)—Association of tall evergreen trees (commonly over 30 m) and associated understory vegetation. This

community is frequently referred to as "the tropical rainforest." In Mexico characteristic species include *Terminalia* amazonica* (J. F. Gmelin) Exell, *Swietenia macrophylla* King, *Brosimum alicastrum* Swartz, *Vochysia hondurensis* Sprague, *Andira galeottiana* Standley, *Bernoullia flammea* Oliver, *Dialium guianense* (Aubl.) Sandwith, *Calophyllum brasiliense* Camb., *Pseudolmedia oxyphyllaria* Donnell Smith, *Calatola laevigata* Standley, *C. mollis* Standley, *Talauma mexicana* (DC.) G. Don, *Ficus tecolutensis* (Liebm.) Miq., and species of *Inga* and *Quercus.**

(7). *Alta Subperennifolia* (High Semi-Evergreen Selva)—In this community 25–50% of the trees are deciduous during the dry season. Characteristic species include *Brosimum alicastrum* Swartz, *Manilkara zapota* (L.) v. Royen, *Mastichodendron capiri* (A. DC.) Cronquist, *Swietenia macrophylla* King, *Bucida buceras* L., *Mirandaceltis monoica* (Hemsley) Sharp, *Carpodiptera ameliae* Lundell. An example of this community occurs in southern Yucatán near the Guatemalan border.

(8). *Mediana Subperennifolia* (Medium Semi-Evergreen Selva)—This community has many species in common with the High Semi-Evergreen Selva, occupying areas of slightly less rainfall. It is defined by trees 15–30 m tall with 25–50% deciduous during the dry season. In southeastern Mexico the community once occupied extensive lowland areas to the north (Tampico to the Orizaba-Córdoba region) and south of Veracruz-Tabasco in the Yucatán lowlands.

(9). *Mediana Caducifolia* (Medium Deciduous Selva)—Trees 15–30 m tall with more than 75% deciduous during the dry season. Common species include *Hymenaea courbaril* L., *Enterolobium cyclocarpum* (Jacq.) Griesb., *Cedrela* odorata* L., *Licania arborea* Seem., *Tabebuia chrysantha* (Jacq.) Nicholson, and *Hura polyandra* Baill. In southeastern Mexico remnants of this selva occur along a broad zone between Campeche northeast to Cabo Catoche.

(10). *Baja Subperennifolia* (Low Semi-Evergreen Selva)—Trees less than 15 m tall and 25–50% of the trees deciduous during the dry season. Characteristic species include *Acacia* pennatula* (Schlecht. & Cham.) Benth., *Acrocomia mexicana* Karw., *Haematoxylum campechianum* L., *Bucida buceras* L., *Metopium brownei* (Jacq.) Urban, and species of *Ateleia*, *Vitex*, *Lonchocarpus*, and *Coccoloba.** In the Tipos de Vegetación the Baja Subperennifolia is shown as scattered isolated stands in southern Yucatán. Breedlove (1973: 159–160) uses "Short-tree Savanna" for comparable vegetation in Chiapas.

(11). *Baja Caducifolia* (Low Deciduous Selva)—Trees less than 15 m tall and almost all deciduous during the dry season. Members of this community include *Lysiloma bahamensis* Benth., *Cordia dodecandra* DC., *Alvaradoa amorphoides* Liebm., *Haematoxylon brasiletto* Karst., *Ceiba acuminata* (S. Watson) Rose, *Bursera* excelsa* (H.B.K.) Engl., *Pistacia mexicana* H.B.K., *Amphipterygium adstringens* (Schlecht.) Schiede, *Cyrtocarpa procera* H.B.K., *Conzattia sericea* Standley, *Pithecellobium flexicaule* (Benth.) Coult., *Olneya tesota* Gray, *Idria columnaris* Kellogg, and *Cercidium.* In southeastern Mexico low deciduous selvas are found in the vicinity of Veracruz and in northern Yucatán Peninsula.

Bosque—Arborescent vegetation of cool, temperate, moderate to high altitudes, generally with one to few dominant tree species.

(12). *de Oyamel*—Coniferous forests of *Abies*.* These are high altitude forest scattered through the mountains of southern Mexico. In southeastern Mexico *Abies religiosa* (H.B.K.) Schlecht. & Cham. is found between Mexico City and Puebla, near Perote, and in the Orizaba-Córdoba region.

(13). *de Cedro y Táscate* (*Cupressus* and *Juniperus* Woodlands)—This community is not extensive in Mexico, but some stands are found just to the northeast of Iguala, and near Perote.

(14). *de Pino* (Pinelands)—This is also a high altitude community, and more or less pure stands of *Pinus** are of scattered and isolated distribution. Examples occur between Mexico City and Puebla, and in the Orizaba-Córdoba region.

(15). *de Pino-Encino* (Pine-Oak Woodlands)—The pine-oak woodlands are among the most widespread of plant communities in Mexico. With differing species composition and proportion of *Pinus** to *Quercus*,* this community occurs at higher elevations ranging from northern Baja California-Arizona-Texas borders southward to Guatemala.

(16). *Caducifolio* (Deciduous Forests)—These forests occur in temperate and humid areas at elevations between 1,000 and 2,000 m along the eastern slopes of the Sierra Madre Oriental from northwest of Ciudad Mante south to the Guatemalan border. Characteristic genera include many disjunct to varying degrees from the deciduous forest of eastern United States, as *Liquidambar*,* *Quercus*,* *Nyssa*, *Carpinus*, *Ostrya*, *Fagus*, *Tilia*, *Cornus*, *Myrica*,* *Ilex*,* *Juglans*,* *Ulmus*,* *Populus*,* in addition to *Ternstroemia*, *Oreopanax*, *Bocconia*, *Engelhardtia*,* *Meliosma*,* *Podocarpus*,* *Cleyera*,* *Cyathea*,* *Eugenia*,* *Tournefortia*,* *Guarea*,* *Hedyosmum*,* *Justicia*,* *Struthanthus*,* *Lycopodium*,* *Selaginella*,* *Psilotum*,* *Alsophila*,* *Dichapetalum*,* and *Weinmannia*.

(17). *de Encino* (Oak Forests)—This community is also widespread from arid zones to the tropics involving different species of *Quercus*.* In southeastern Mexico oak woodlands are found east of Tuxtepec, just east of Coatzacoalcos inland toward San Andrés Tuxtla, and at the Veracruz-Oaxaca border in the Isthmus of Tehuantepec.

(18). *Mezquital*—Mesquite (*Prosopis*) shrub vegetation of northern (along the Texas-Arizona border) and central (Guanajuato-Querétaro region) Mexico.

(19). *Chaparral*—This is a shrub community common in northern Mexico frequently found at lower elevations of mountainous regions at the contact with arid flat lowlands. Characteristic genera are *Quercus*,* *Arctostaphylos*, *Cercocarpus*, *Amelanchier* and *Adenostoma*.

Matorral.—Thicket.

(20). *Submontano* (Submontane Thicket)—Vegetation of low trees 3–5 m tall, briefly deciduous during the dry season, occurring in arid regions of northeastern Mexico. The principal genera include *Leucaena*, *Cordia*, *Bumelia*, *Helietta*, *Acacia*,* *Opuntia*, *Gochnatia*, *Celtis*,* *Flourensia*, *Mimosa*,* *Colubrina*, *Lysiloma*, *Pseudomodingium*, *Pistacia*.

(21). *Crasicaule*—A community characterized by large cylindrical or flat-stem cacti of *Lemaireocereus*, *Neobuxbaumia*, *Myrtillocactus*, *Escontria*, *Car-*

negiea, Cephalocereus, and *Opuntia.* In south-central Mexico the Matorral Crasicaule is especially well developed along the Tehuacán Valley between Huajuapan de León and the city of Tehuacán.

(22). *Desértico Rosetófilo*—A community of dry regions with plants of rosette growth form. Genera include *Yucca, Agave, Hechtia, Dasylirion, Beaucarnea,* and *Nolina.* An example of the Matorral Desertico Rosetofilo is found in south-central Mexico just north of Tehuacán.

(23). *Desértico Micrófilo*—A vegetation type found in dry areas and characterized by plants with small leaves. Common genera include *Larrea, Flourensia, Allionia,* and *Celtis.**

Zacatal.—Grasslands.

(24). *Pastizal*—Dry grasslands of central and northern Mexico consisting of *Bouteloua, Muhlenbergia, Sporobolus, Hilaria, Distichlis, Lycurus, Heteropogon, Elyonurus, Buchloe, Eragrostis, Spartina, Cathestecum,* and *Opizia.*

(25). *Zacatonal*—Grasslands of colder higher elevations with more robust grasses of *Muhlenbergia, Festuca, Stipa,* and *Calamagrostis.*

VEGETATION OF VERACRUZ

The modern vegetation of Veracruz is known through several regional studies (e.g., Gómez-Pompa, 1966; Gómez-Pompa et al., 1964; Gómez-Pompa & León Cázares, 1970; León Cázares & Gómez-Pompa, 1970), and has recently been summarized by Gómez-Pompa (1973). He recognizes 22 communities, and in the following summary these are correlated with the classification terminology used in the *Tipos de Vegetación.*

Forests (Bosques).—

(1). *Needle-Leaved Forests* (Bosque de Oyamel, de Pino, de Pino-Encino) and *Scale-Leaved Forests* (Bosque de Cedro y Táscate)—These are high-altitude coniferous forests at elevations between 3,000 and 4,000 m, with an average annual temperature of about 4–11°C. The dominant species is *Pinus** *hartwegii* Lindl., with *P. montezumae* Lamb. and *Abies** *religiosa* (H.B.K.) Schlecht. & Cham. Stands are found at the Pico de Orizaba and in the Cofre de Perote. Fossil pollen of *Picea,** not present in the modern flora of Veracruz, occurs in the Paraje Solo Formation and probably grew in the higher altitude portions of the Needle-Leaved Forest. Fossil pollen of a few wide-ranging plants that reach into the Needle-Leaved Forest, such as *Alnus** and *Smilax,** has also been recovered.

At lower elevations of 2,000–3,000 m, pine is mixed with *Quercus** to form the wide-spread Bosque de Pino-Encino. Gómez-Pompa (1973: 95) gives a climatograph from Acultzingo showing an average annual temperature of 17.4°C (minimum ca. 13°C) and a yearly rainfall of 723.7 mm. The pine species are *P. pseudostrobus* Lindl., *P. teocote* Cham. & Schlecht., *P. rudis* Endl., *P. strobus* L. var. *chiapensis* Martínez, *P. oocarpa* Schiede, *P. ayacahuite* Ehrenberg, *P. leiophylla* Schlecht. & Cham., and *P. patula* Schlecht. & Cham. The common

species of oak are *Q. candicans* Nee, *Q. xalapensis* Humb., *Q. castanea* Nee, *Q. crassifolia* Humb., *Q. mexicana* Humb., and *Q. excelsa* Liebm. Associated with the *Quercus-Pinus* Forest are two genera represented by pollen in the Paraje Solo Formation, *Alnus* arguta* (Schlecht.) Spach, and *Smilax spinosa* Mill.

A small scale-leaved forest of *Juniperus deppeana* Steud. occurs near Perote. This is a community of drier climates, found near the contact of temperate pine-oak and more arid vegetation at about 2,500 m. Other species include *Pinus cembroides* Zucc., *Nolina parviflora* (H.B.K.) Hemsley, *Quercus microphylla* Nee, and *Sophora secundiflora* (Ortega) Lag. At present, pollen of *Juniperus*, *Nolina* and *Sophora* has not been found in the Paraje Solo microflora.

(2). *Broad-Leaved Forests* (Bosque de Encino)—These forests are commonly dominated by *Quercus.** At higher elevations they grade into pine-oak communities, but in warm lowlands they constitute a more distinct community. The principal species is *Q. oleoides* Cham. & Schlecht. Also present are other plants also represented by pollen in the Paraje Solo Formation, including *Alchornea* latifolia* Swartz, *Sapium* lateriflorum* Hemsley, and *Coccoloba* barbadensis* Jacq.

(3). *Deciduous Forests* (Bosque Caducifolio)—Gómez-Pompa (1973: 102) provides a climatograph from Huatusco, elevation 1,344 m, within the Deciduous Forest. The temperature range is from 15°C (December–January) to 21°C (May–June), with an annual average of 15.7°C. Yearly rainfall is 1,745 mm, falling mainly from April through October. The characteristic deciduous species is *Liquidambar* macrophylla* Oerst. mixed with *Quercus** (*Q. affinis* Schwidw., *Q. ocoteafolia* Liebm., *Q. skinneri* Benth., *Q. brachybotrya* Zucc., *Q. corrugata* Hook., and *Q. pilarius* Trel.). Both *Liquidambar* and *Quercus* occur in the Paraje Solo Formation together with several others presently found in the Deciduous Forest: *Cleyera* serrulata* Choisy, *Cyathea* fulva* (Mart. & Gal.) Fee, *Eugenia* trunciflora* (Schlecht. & Cham.) Berg, *E. mexicana* Steud., *Ilex* vomitoria* Ait., *Juglans* pyriformis* Liebm., *Lycopodium* cernuum* L., *Meliosma* alba* (Schlecht.) Walp., *Podocarpus* matudai* Lundell, *Tournefortia* petiolaris* DC., *Ulmus* mexicana* Liebm., *Guarea* chichon* C. DC., *Engelhardtia* mexicana* Standley, *Psilotum* complanatum* Swartz, *Selaginella,* Alsophila,* Dichapetalum,* Hedyosmum,* Justicia** (widespread), *Populus** (riparian, widespread), and *Struthanthus.**

Selvas.—

(4). *High Evergreen Selvas* (Selva Alta Perennifolia)—In Veracruz this community occurs where annual precipitation ranges from a minimum of about 2,500 mm (2,726 mm at Coatzacoalcos, elevation 14 m) to 5,000 mm (4,439 mm at Coyame, elevation 340 m) with no pronounced dry season. Temperatures are from about 20°C (December–January) to 27°C (April–May) with a yearly average between 23–25°C. The dominant tree species are frequently 25–30 m tall and approximately 80% or more of the component species are evergreen. Characteristic members of the High Evergreen Selva are *Terminalia* amazonica* (J. F. Gmelin) Exell, *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoulia flammea* Oliver, *Brosimum alicastrum* Swartz, *Ficus tecolu-*

tensis (Liebm.) Miq., and *Pseudolmedia oxyphyllaria* Donnell Smith. A few associated genera have been found in the Paraje Solo microflora, including *Cupania* dentata* DC., *Guarea* chichon* C. DC., *G. tonduzii* C. DC., *G. bijuga* C. DC., *G. glabra* Vahl, *Matayba* oppositifolia* (Rich.) Britton, *Podocarpus* guatemalensis* Standley, *Alchornea* latifolia* Swartz, *Astrocaryum* mexicanum* Liebm., *Bursera* simaruba* (Swartz) Sarg., *Chamaedorea* alternans* Wendl., *C. ernesti-agusti* (Wendl.) Oerst., *C. lindeniana* Wendl., *C. oblongata* Mart., *C. tepejilote* Liebm., *Hampea* nutricia* Fryxell, *Sapium* nitidum* (Monach.) Lundell, and *Tetrorchidium* rotundatum* Standley.

(5). *High Semi-Evergreen Selvas* (Selva Alta Subperennifolia)—The deciduous habit of up to 50% of component species characterizes the High Semi-Evergreen Selva. The association is found in areas of slightly reduced rainfall (minimum ca. 1,800 mm per year) or in more humid areas on well-drained soils. The dominant species is frequently *Brosimum alicastrum* Swartz, with *Ficus tecolutensis* (Liebm.) Miq., *Bursera* simaruba* (Swartz) Sarg., *Achras zapota* L., *Cedrela* odorata* L., *Coccoloba,* Croton nitens* Swartz, *Bernoullia flammea* Oliver, *Sapium* lateriflorum* Hemsley, *Lonchocarpus*, *Mirandaceltis monoica* (Hemsley) Sharp, *Castilla elastica* Cerv., *Zuelania guidonia* (Swartz) Britton & Millsp., *Guarea* chichon* C. DC., *Pithecellobium insigne* Micheli, *Tabernaemontana alba* Mill., *Iresine* nigra* Uline & Bray, *Alchornea* latifolia* Swartz, *Cupania* dentata* DC., *Ilex* condensata* Turcz., *Protium* copal* (Schlecht. & Cham.) Engl., and *Chamaedorea* lunata* Liebm.

(6). *Medium Semi-Evergreen Selvas* (Selva Mediana Subperennifolia)—In Veracruz this is a transition community composed of species from the tall and low selvas occupying sites intermediate between these humid and drier associations.

(7). *Low Evergreen Selva*—At the top of Volcán San Martín a low, dense vegetation with numerous epiphytes occurs (the mossy or elfin forest), composed of *Clusia*, *Elleanthus*, *Gaultheria*, *Ilex,* Litsea*, *Monnina*, *Myrica,* Oreopanax*, *Palicourea*, *Rapanea*, *Saurauia*, *Senecio*, and *Viburnum*. The Low Evergreen Selva is an unusual type of community with restricted distribution, and is not recognized as a distinct association in the *Tipos de Vegetación* (scale 1: 2,000,000). Other than *Ilex* and *Myrica*, which occur in several communities, elements of the elfin forest are not represented in the Paraje Solo microflora.

(8). *Low Semi-Evergreen Selvas* (Selva Baja Subperennifolia)—Agriculturally poor soils and milpa farming practices are characteristic of regions with Low Semi-Evergreen Selvas in Veracruz. Consequently, there is some uncertainty as to the naturalness of this community and the importance of anthropogenic factors in determing its range. Rainfall is relatively low (1,400–1,800 mm; Gómez-Pompa, 1973: 119–121), and the community is occasionally recognized as a type of savanna. Characteristic species are *Acrocomia mexicana* Karw., *Byrsonima crassifolia* (L.) DC., *Curatella americana* L., *Psidium guajava* L., *Crescentia cujete* L., and *Coccoloba* barbadensis* Jacq. Only the latter occurs in the upper Miocene assemblage at Coatzacoalcos, and it ranges into other types of vegetation.

(9). *Low Deciduous Selvas* (Selva Baja Caducifolia)—These selvas occur

where precipitation is less than 1,500 mm per year, and a dry season often of six months or more is present. Most trees are less than 10 m tall and leafless during the dry season (November through March; Gómez-Pompa, 1973: 121–124). Dominant species in the Low Deciduous Selvas include *Cordia dodecandra* DC., *Crescentia alata* H.B.K., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Piscidia piscipula* (L.) Sarg., *Tabebuia chrysantha* (Jacq.) Nicholson, and *T. rosea* (Bert.) DC. None of these genera are represented by pollen in the Paraje Solo microflora. The pollen of a few genera associated with the Low Deciduous Selva (and commonly ranging into other types) has been recovered, including *Acacia* cornigera* (L.) Willd., *A. farnesiana* (L.) Willd., *Bursera* bipinnata* Engl., *B. fagaroides* (H.B.K.) Engl., *B. simaruba* (Swartz) Sarg., *Casearia* nitida* (L.) Jacq., *Celtis* iguanaea* (Jacq.) Sarg., *Comocladia* engleriana* Loes., *Cupania* macrophylla* A. Rich., *Daphnopsis* brevifolia* Nevling, *Eugenia* liebmanni* Standley, and cf. *Sapium** sp.

(10). *Low Thorn Selvas* (Matorral Submontano)—According to Gómez-Pompa (1973: 124–126): "This vegetation type is found in the driest regions of lowland areas where precipitation is under 1000 mm and where the dry season is long and pronounced. These regions also have the lowest winter temperatures in the lowlands. The combined effect of these highly selective factors gives rise to the very characteristic flora, which is a combination of floristic elements from the more humid areas in the south and the Tamaulipas deserts in the north." Among the characteristic genera are *Abutilon*, *Acacia*,* *Acanthocarpus*, *Boerhavia*, *Cordia*, *Coursetia*, *Chlorophora*, *Citharexylum*, *Croton*, *Erythroxylon*, *Eugenia*,* *Guazuma*, *Jacquinia*, *Malpighia*,* *Mimosa*,* *Morrisonia*, *Nopalea*, *Parkinsonia*, *Phyllanthus*, *Plumbago*, *Pithecellobium*, *Randia*, *Solanum*, *Schoepfia*, *Trichilia*, and *Zyzyphus*.

(11). *Palm Stands* (Palmar).—Three genera dominate the principal palm stands in Veracruz, *Scheelea liebmanii* Becc., *Sabal mexicana* Mart., and *Paurotis wrightii* (Griseb. Wendl.) Britton. None of these have been found as yet in the Paraje Solo microflora. Genera commonly associated with the palm stands are *Albizzia*, *Bunchosia*, *Citharexylum*, *Cupania*,* *Pleuranthodendron*, *Sapindus*, *Stemmadenia*, *Trophis*, *Pithecellobium*, *Zanthoxylum*, *Ruprechtia*, *Randia*, and *Acacia*.* Although six types of palm pollen have been distinguished in the microfossil assemblage (Table 1), neither individually nor collectively do they reach percentages that would reflect palm-dominated vegetation in the immediate vicinity.

Grasslands (Zacatal).—

(12). *Savannas* (Sabana)—Most genera of grasses cannot be recognized on the basis of pollen characters, especially at magnifications of the light microscope. Consequently the various communities in which the Gramineae are prominent cannot easily be distinguished in the microfossil record. At Site 4 grass pollen reaches the highest percentages (sample 19, 27%; sample 21, 45%; sample 30, 29%; sample 33, 30%). One community in which grasses may reach these percentages is the savanna. León Cázares & Gómez-Pompa (1970) describe a savanna near Coatzacoalcos. The dominant grass is *Paspalum pecti-*

natum Nees, and the common shrub is *Curatella americana* L. In the Short-Tree Savanna described by Breedlove (1973: 159–160) from Chiapas, the common trees and shrubs are *Byrsonima crassifolia* (L.) DC., *Crescentia cujete* L., *C. alata* H.B.K., and *Curatella americana* L. Other nongrass genera include *Piscidia, Alvaradoa, Kyllinga, Acisanthera, Ageratum, Cassia, Chamaesyce, Coccocypselum, Cologania, Conostegia, Crotalaria, Diodia, Euphorbia, Hibiscus,* Hyptis, Melochia, Mimosa,* Myrica,* Paurotis, Polygala, Rhynchanthera, Russelia, Sauvagesia, Spermacoce, Schultesia, Xyris,* and *Zexmenia.* The poor representation of genera in the microflora, other than grasses, characteristic of savannas suggest this type of community was not prominent in the vicinity during the upper Miocene.

(13). *Temperate Grasslands*—Because of the agricultural practices of sedentary populations occupying the lowlands of Veracruz for at least 5,000 years, grasslands (like savannas and palm stands) are highly modified. At present natural Temperate Grasslands are poorly represented in Veracruz, but the Valley of Perote may have supported such a community in earlier times (Gómez-Pompa, 1973: 132). Remnants of a Temperate Grassland are reflected by the presence of *Bouteloua curtipendula* (Michx.) Torr., *B. gracilis* (H.B.K.) Lag. ex Steud., *Microchloa kunthii* Desv., and *Setaria geniculata* (Lam.) Beauv. Nongrass genera associated with remnants of Temperate Grasslands are *Anthericum, Asclepias, Bulbostylis, Cologania, Commelina, Cyperus* (Cyperaceae*), *Eryngium, Heliotropium, Ipomoea, Nemastylis, Ophioglossum, Oxalis, Piranopappus, Quercus,* Ranunculus, Selaginella,* Sisyrinchium, Stevia, Tridax,* and *Verbena.*

(14). *Saline Grasslands*—These communities may be temperate and upland, with high salinity due to evaporation, or lowland and coastal periodically inundated by marine waters. The former are characterized by *Distichlis spicata* L., and the latter by *Spartina* (*S. alterniflora* Loisel., *S. spartinae* (Trin.) Merr.; the "espartal"). Associated genera are *Actinella, Alternanthera* (Amaranthaceae; represented as ChenoAm.*), *Aphanostephanus* (*Compositae**), *Atriplex, Croton, Cuscuta, Dichondra, Erodium, Gomphrena, Heliotropium, Houstonia, Plantago, Sanvitalia, Verbena, Batis, Borrichia,* and *Salicornia.*

(15). *Nolina-Hechtia-Agave Desert* (Matorral Desértico Rosetófilo).—Evidence for arid or semiarid vegetation during the upper Miocene is meager for southern Veracruz. In the north near the border with Puebla, at an elevation of about 23 m, there is a desert of *Nolina parviflora* (H.B.K.) Hemsley, *Hechtia roseana* L., and *Agave obscura* Schiede. Average annual temperature is 14.9°C, with extremes of about 11°C (December–January) to 16°C (May–June). Other genera are *Adolphia, Aneilema, Aristida, Chrysactenia, Bouvardia, Dalea, Dasylirion, Dyssodia, Juniperus, Loeselia, Lycurus, Mamillaria, Salvia, Stipa,* and *Tradescantia.* With the possible exception of generically undifferentated members of the Gramineae and Compositae none of these dominant (*Nolina, Hechtia, Agave*) or associated genera are presently known from the Paraje Solo Formation.

(16). *Thorn Scrub* (Matorral Crassicaule).—Two types of thorn scrub occur in Veracruz, one at higher elevations (1,500 m or more) and another less well defined one in the lowlands (less than 500 m; Gómez-Pompa, 1973: 137).

TABLE 1. Distribution of identified taxa of pollen and spores among collection sites, Paraje Solo Formation. Figures represent percent of total at each locality; x indicates pollen and spore types present, but not encountered in counts of 100.

	Site 1			Site 2						Site 3		Site 4							Site 5					Site 6				
Taxa	1	2	4	5	6	7	8	9	10	13	15	17	19	21	25	30	32	33	34	35	37	38	40	44	45	49	51	54
Psilotum													x				7	5			1							
Lycopodium																						x						
Selaginella		1					x	1	1														x					
Alsophila		x													x				x									
Cyathea										x																		
Hemitelia	4					x	x	x	x						x				1	x	x		x		x			
Dicranopteris													x			x												
Pityrogramma				x																								
Lomariopsis (*Stenochlaena*)							2												1									
Ceratopteris		x																							2	2		
Pteris																												
type 1									x																			
type 2							x			x																		
type 3															x													
Other monoletes																												
type 1	48	x	1	2	1	3	3	3	3	4	6						x	2	10	1	1		3			4		
type 2							1	3	1	x																		
type 3						1				1					x				1		1				1			
type 4	6	x				x		1	1						x	x			1		1							
type 5									x																			
type 6				1				2	1	3	40		5	4		3	3		5	1		1	3	1	6			
Other triletes	7	3			2	2	2	3	2						1	3	2	1	2		1		2	1	3			
Abies		x															x											
Picea		x		1				1	x												x							

TABLE 1. (Continued).

Taxa	Site 1			Site 2						Site 3		Site 4							Site 5					Site 6				
	1	2	4	5	6	7	8	9	10	13	15	17	19	21	25	30	32	33	34	35	37	38	40	44	45	49	51	54
Pinus type 1														1									x					
Pinus type 2			1																									
Podocarpus		x				1		x		x		1	1		x		1	x	1		x	x	2		x		x	
Spathiphyllum							1	x											x									
Cyperaceae														x		x							x					
Rajania		1	4		1			1					5	3	6	1	7	4										
Gramineae		11	3	1	x	x	x	10	1	17	16	7	27	45	3	29	3	30	4	x	1	1	4	19	5	18	2	2
Smilax			2						x														x					
cf. *Astrocaryum*																												
cf. *Brahea*	6																											
cf. *Chamaedorea*			x					2																				
cf. *Maximiliana*		x																										
cf. *Attalea*								1																2	6			
Palmae (cf. *Calamus*? type)				1	2	1	2	1	1												1							
Bravaisia																			1									
Justicia		x								1	x	x		x		x		x				x						
Iresine							x																					
ChenoAm.		x							x			x		x							x							
Comocladia					1		1		1										x	x								
Ilex		1						x	x										1	x						x		
Alnus																						x						
Tournefortia										x						x												
Bursera	4	x							x														x				x	

TABLE 1. (Continued).

Taxa	Site 1			Site 2						Site 3		Site 4							Site 5					Site 6				
	1	2	4	5	6	7	8	9	10	13	15	17	19	21	25	30	32	33	34	35	37	38	40	44	45	49	51	54
Protium	2					1	2								1				5		1							
Hedyosmum										2																		
Combretum/Terminalia										9	x	25	7	1	1		4	1										
Laguncularia		7				1				19	14	30	10		56	9	20	13	19	1			12					
Compositae																												
type 1		1									x		x					2										
type 2					1				x			5				2	3	1										
type 3										x		2			x		1	1	1	x		x						
type 4									x			x	1	1														
type 5					1	1				x		18	20	12	22	27	13	6	1									
type 6		1	1					1	x	3			1	2		1	x					1			1			x
Dichapetalum															x													
Alchornea			x	x		x		x	x	2	4							2	x	x		1	2				x	
cf. *Bernardia*		x				x		x	x																			
cf. *Sapium*	3	1					x	x	x		x	x																
cf. *Stillingia*							x																					
cf. *Tetrorchidium*																			1									x
cf. *Tithymalus*											1																	
Quercus		1	x	5	1	5	4	3	2	7	2	1	7	12	3	5	7	13	3			1		30	34	33	4	1
Casearia				x	1																							
Laetia							x																					
Liquidambar		x	x																									
Symphonia		x																										
Engelhardtia		1	1	2		4	4	3	2	6	1	2	1		x		2	1	13	1	3	1	x	1	5	x	2	1
Juglans									x																			x
Gustavia															x													
cf. *Acacia*										1					x									x				
Desmanthus										1	x																	
Mimosa													x															
Utricularia													1					x										
Struthanthus		x	2	1	x	1	2					x	1		x		1				1	1	1			8		
Cuphea															x													

TABLE 1. (Continued).

Taxa	Site 1			Site 2						Site 3		Site 4							Site 5					Site 6				
	1	2	4	5	6	7	8	9	10	13	15	17	19	21	25	30	32	33	34	35	37	38	40	44	45	49	51	54
cf. *Hiraea*		x																										
cf. *Malpighia*		x	1	x				x		1														4	6			
Malpighiaceae (cf. *Mezia*? type)							1						x	1									1					
Hampea/Hibiscus		1		1					2								x	1	1					2				
Cedrela					1	2	x		1										1		1			1	2			
Guarea					x					x																		
Myrica						1	x	4	x		x			1	x		2	x										
Eugenia/Myrcia		3	2		1	2		x	x	6		1	3						1		1			3	5	16		1
Ludwigia						x	x	x			2		1			x	x	x					2		x		x	
Passiflora		1											x															
cf. *Bredemeyera*										1								x										
cf. *Securidaca*										x			x															
Coccoloba		x	4						x			x	x	2	x	9	7	3			x							
Thalictrum										x		x					1	1	1									
Rhizophora		63	62	80	78	68	69	47	77	4	5	2			3	x	1	1	14	96	84	91	10	14	x	8	86	91
cf. *Alibertia*											x					1		x				x						
Borreria										x	x																	
Faramea							2	1		x																		
Terebrania						1																						
Populus	x									x																		
Allophylus									x						x													
Cupania	x					x			x																			
Matayba	x			1					1						1													
Meliosma						1										1			1				x					
cf. *Paullinia*		x					x		x	x					x										1	1		
Serjania		1								x					x						1					x		
Buettneria										x											x							
Cleyera												x						x										
Daphnopsis							x					1		1	x		1							4	5			
Celtis	x				x	x	3	1				x																
Ulmus							x											1		x	x	x			x		x	x

Characteristic genera in the former are *Agave*, *Asclepias*, *Bouvardia*, *Buddleia*, *Croton*, *Echinocactus*, *Eupatorium*, *Juniperus*, *Karwinskia*, *Mammillaria*, *Myrtillocactus*, *Notholaena*, *Opuntia*, and *Quercus*.* In the latter are *Bursera*,* *Capparis*, *Capraria*, *Condalia*, *Esenbeckia*, *Karwinskia*, *Nopalea*, *Prosopis*, *Pithecellobium*, *Randia*, *Yucca*, and *Zanthoxylum*. With the possible exception of the wide-ranging *Quercus* (represented in the thorn scrub by *Q. eduardii* Trel.) and *Bursera* [represented by *B. simaruba* (Swartz) Sarg.], and generically undifferentiated Compositae, none of the above have been recovered as yet from the Paraje Solo microflora.

(17). *Swamp Vegetation*.—Two types of swamp communities are present in Veracruz. One is the Inland Swamp occurring in fresh-water environments, and the other is the coastal brackish Mangrove Swamp.

(18). *Inland Swamps* (Popal)—The composition of the Inland Swamp varies and community names are based on the local dominant. A common member is *Thalia geniculata* L. (popal), associated with *Bactris*, *Cyperus* (Cyperaceae*), *Eleocharis*, and *Pontederia*.

(19). *Mangrove Swamps* (Manglar)—Deposition of the Paraje Solo sediments took place in or near a coastal, marine-brackish water environment, as evidenced by the abundance of *Rhizophora** and *Laguncularia** pollen. Modern members of the mangrove swamp include *Rhizophora mangle* L., *Laguncularia racemosa* (L.) Gaertn. f., *Avicennia germinans* L., and *Conocarpus erecta* L. Pollen of *Avicennia* and *Conocarpus* have not been identified as yet from the Paraje Solo Formation, but, even in modern communities, all four mangroves are not consistently present. Vázquez (1971), for example, did not find *Conocarpus* in mangrove swamps near Mandinga, Veracruz.

Another vegetation type, intermediate between the fresh-water Inland Swamps and the brackish Mangrove Swamps, is one characterized by *Pachira aquatica* Aubl. These communities are mainly inland but can tolerate occasional inundation and slightly brackish waters. Associated genera include *Acrostichum*, *Amerimon*, *Annona*, *Avicennia*, *Clerodendrum*, *Dalbergia*, *Diospyros*, *Ficus*, *Hibiscus*,* *Laguncularia*,* *Pithecellobium*, *Piper*, *Randia*, *Rhabdadenia*, *Rhizophora*,* and *Sapium*.*

The *Thalia* and *Pachira* swamps are of local and scattered occurrence in Veracruz. Their restricted distribution, together with generally low pollen production, presence of stenopalynous grasses, sedges, composites, and chenoams, and the poorly developed exine of some species may account for their low numerical representation in sediments deposited under coastal marine-brackish water conditions. In contrast, *Rhizophora* (maximum 96%) and *Laguncularia* (maximum 56%) produce moderate to large amounts of pollen and being locally dominant are over-represented considering the regional vegetation of southern Veracruz.

(20). *Paramo Vegetation* (Zacatonal).—The Paramo is a high-altitude community between timber line and the zone of permanent snow. Since the Paraje Solo sediments were deposited at sea level, the absence of pollen of Paramo

genera, like elements of the *Thalia* and *Pachira* swamps, is not significant. Paleobotanical data presently available for southern Veracruz is not adequate to assess the presence or absence of these communities. The Sierra Madre Oriental reached significant heights at the end of the Cretaceous, and there is no reason to assume the absence of Paramo vegetation by the end of the Miocene. Also, swamp communities, unlike savannas and palm stands, are not as suspect of anthropogenic control or influence and were likely present at various times and places during the Cenozoic.

(21). *Coastal Dunes Vegetation.*—This community includes a number of grasses (*Andropogon glomeratus* (Walt.) B.S.P., *A. litoralis* Nash, *Eragrostis domingensis* (Pers.) Steud., *Panicum repens* L., *Paspalum vaginatum* Swartz, *Sporobolus virginicus* (L.) Kunth, *Spartinia patens* (Ait.) Muhl., *Uniola paniculata* L.), composites (*Bidens squarrosa* H.B.K., *Iva asperifolia* Less., *Palafoxia texana* DC.), sedges (*Cyperus articulatus* L., *C. ligularis* L., *Fimbristylis spathacea* Roth) and ChenoAms. (*Amaranthus gregii* S. Watson). These families are well represented in the fossil microflora, but individual genera cannot consistently be distinguished on the basis of pollen characters. It is likely, however, given the depositional environment of the Paraje Solo sediments, that coastal dune and the related island vegetation (Gómez-Pompa, 1973: 143), is represented in the microflora. Other genera occuring in these communities recovered from the Paraje Solo Formation are *Acacia,** *Casearia,** *Coccoloba,** *Iresine,** *Laguncularia,** *Terminalia,*[4] and *Tournefortia.**

(22). *Aquatic Vegetation Types.*—Pollen of various elements comprising aquatic vegetation is poorly represented in the Paraje Solo microflora. Spores of the floating fern *Ceratopteris,** and pollen of *Utricularia** have been recovered. Other genera common to the aquatic flora of Veracruz are not known from the microflora (e.g., *Halodule, Thalassia, Halophila, Ruppia, Syringodium, Crinum, Pontederia, Sagittaria, Typha, Nymphaea, Cabomba, Ceratophyllum, Najas, Bocopa,* and *Pistia*). This does not preclude the presence of these communities, however, since for reasons mentioned in section 20, pollen of aquatic plants are often poorly represented in lignites.

The survey of modern vegetation in Mexico serves to identify the geographic region having closest floristic similarity to the Miocene communities. Although some vegetation types are wide-ranging (e.g., Bosque de Pino y Encino), clearly, the paleocommunities represented in the Paraje Solo microflora are most similar to the modern vegetation of southeastern Mexico. Of the 69 identified genera listed in Table 1 (excluding tentative cf.-identifications), only 5 are no longer present in Veracruz (Table 4), and two of these (*Ceratopteris, Laetia*) are known from adjacent states. The genus *Symphonia*, known for several years in the fossil flora, has now been found in the modern vegetation (Gómez-Pompa, personal communication, 1974). Thus, the similarity in generic composition of the Paraje Solo assemblage to the present vegetation in Veracruz is

[4] The lowland species *Terminalia catappa* L. in Veracruz is introduced.

clearly evident, and makes possible rather precise reconstruction of the paleocommunities and paleoenvironmental conditions.

AGE AND STRATIGRAPHY OF THE PARAJE SOLO FORMATION

Sediments exposed in the vicinity of Coatzacoalcos are of Cenozoic age, ranging from the Lutitas Nanchital Formation (Paleocene-Eocene) to the Acalapa Formation (Pliocene), with Quaternary sandstones and deltaic deposits from the Coatzacoalcos and Uxpanapa rivers currently being deposited along the coast and in bordering mangrove swamps. In the immediate vicinity lignites as distinct lithological units are confined to the Paraje Solo Formation as beds 2.5–20.5 cm thick in fine to coarse-grained sediments.

The Paraje Solo Formation is underlain by the Filisolo and Concepción Superior formations, and overlain by the Agueguexquite Formation:

Acalapa
Cedral
Agueguexquite
Paraje Solo
Filisolo
Concepción Superior
Concepción Inferior
Encanto
Depósito
La Laja
Lutitas Nanchital

Both the Paraje Solo and Filisolo Formations lack fossil faunas. The overlying Agueguexquite Formation was originally assigned to the upper Miocene based on benthic microfossil assemblages, and the Paraje Solo Formation was regarded as middle Miocene (Stratigraphic Chart, Petróleos Mexicanos Zona Sur; Gutiérrez Gil, pers. comm., 1964). The plant microfossils suggested a younger age, particularly in the presence of Compositae pollen of the Lactuceae type. In the southern Gulf-Caribbean region pollen of the Lactuceae does not appear in stratigraphically meaningful amounts until the upper Miocene. Its common occurrence in the Paraje Solo Formation (Figs. 86–87) at several sites (Table 1), together with the modern aspect of the total assemblage, indicated an age no older than upper Miocene. Subsequently an abundant fauna containing the planktonic *Globorotalia margaritae*, regarded as a guide fossil to the upper Miocene of southern coastal Mexico, has been found in the Concepción Superior Formation. Revision of the benthic and planktonic foraminifera of the Agueguexquite Formation has resulted in its reassignment to the basal Pliocene. This formation is separated from the underlying Paraje Solo Formation by an unconformity. Thus the stratigraphic relationships, as presently understood, place the Paraje Solo Formation, lacking a fossil fauna but containing Lactuceae pollen, between the upper Miocene Concepción Superior and the Pliocene Agueguexquite Formation, both dated on the basis of benthic and planktonic foraminifera. This suggests an age of upper to uppermost Miocene for the Paraje Solo Formation. On the basis of this revised age assignment, the pollen and spores of the Paraje Solo Formation represent remnants of a vegetation occupying southeastern coastal Mexico and the eastern slopes of the Sierra Madre Oriental approximately 10 to 12 million years ago.

Materials and Methods

Reference Collection of Modern Taxa: Identification of plant microfossils was by comparison with modern palynomorphs in a pollen and spore reference collection. The collection numbers about 15,000 species and has been assembled through exchange and processing of herbarium material. Slides for our laboratory were processed by the KOH-acetolysis technique, mounted unstained in glycerine jelly, and sealed with diaphane. A few of the exchange slides are mounted in silicone oil. All material used for identification purposes has a voucher in one of several herbaria (A, GH, MICH, MO, TEX, US).

Sample Preparation of Fossil Material: Processing procedures for the lignites, fine-grained lignitic sandstones, and siltstones generally follow techniques described by Gray (1965). Surfaces were scraped and washed with distilled water, crushed, and sonicated for 1–3 min. The residues were rinsed in 10% HCl (for removal of carbonates), washed 6–8 times with distilled water, transferred to polyethylene beakers, and covered with HF for 12 h (removal of silicates). Following the HF treatment the samples were rinsed and covered with Schulze solution (mixture of saturated $KClO_3$ to equal parts of HNO_3) for 1–24 h depending on the amount of organic material present. The purpose of the Schulze solution is to oxidize lignins present in the matrix. Following oxidation, samples were treated with an acetolysis mixture (9 parts of acetic anhydride to 1 part of concentrated sulfuric acid) for 1–3 min for removal of cellulose debris by esterfication. After acetolysis, samples were rinsed in glacial acetic acid, distilled water, 50% glycerol (for swelling of compressed pollen and spores), and drained for 1 h. The concentrated pollen residues were mounted unstained in glycerine jelly and sealed with diaphane. The plant microfossils were photographed with a Zeiss microscope and automatic camera using Panatomic-X film. The microfossils are illustrated in Figs. 6–255.

The Collection Localities

The general depositional environment of the Paraje Solo lignites can be estimated from conditions presently prevailing at sites of comparable sedimentation. Studies of peat deposition in warm-temperate regions (e.g., Scholl, 1964a, 1964b; Cohen & Spackman, 1972) indicate that the peat precursors of lignites dominated by mangroves (*Rhizophora, Laguncularia, Avicennia, Conocarpus, Pelliciera*) are paralic (marine coastal) and frequently form under deltaic environments. Freshwater streams emptying into ocean waters create the brackish conditions favorable to mangrove vegetation. In southern Veracruz these conditions are provided by the major drainage systems of the ríos Papaloapan, Coatzacoalcos, Uxpanopa, and Tonala emptying into the Gulf of Mexico in the vicinity of Coatzacoalcos. This is generally a low-energy type of environment with regards to sediment transport where autochthonous peat and fine-grained sediments can accumulate. The accumulation of these sediments is favored by a broad, low, relatively flat coastal plain that extends along the coast of Veracruz. Relatively slight eustatic changes in sea level or local uplifts and subsidence associated with vulcanism (e.g., rise of the Sierra de Los

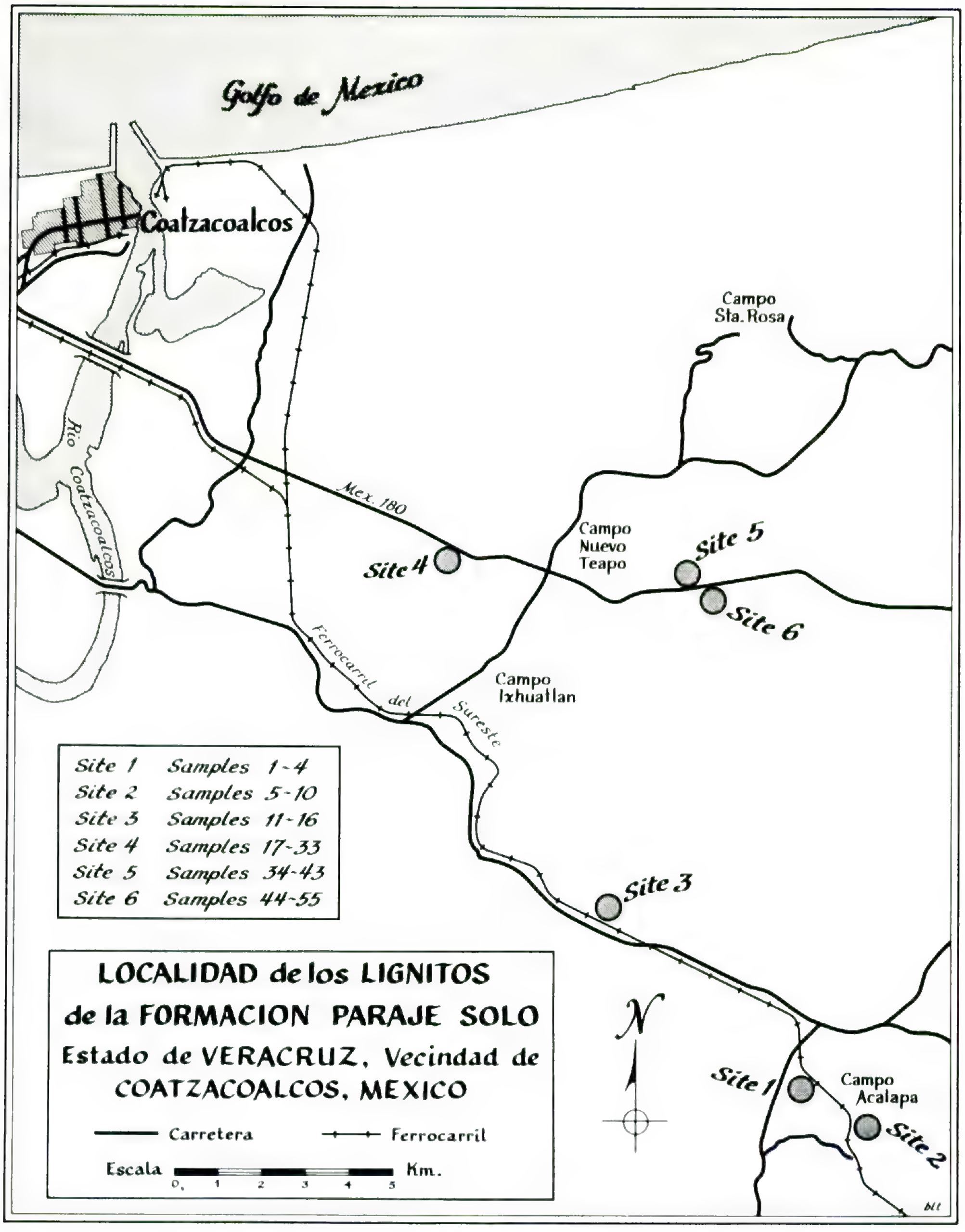


FIGURE 2. Map of collecting localities in the upper Miocene Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico.

Tuxtlas near Coatzacoalcos) affect extensive inland areas of the coastal plain. Marine transgressions depositing coarser-grained sandstones, occasional pirating of coastal sections of drainage systems, and marine invasion of paludal (swamp) environments are characteristic of mangrove habitats. In areas at and just beyond high tide some evaporation of interstitial water results in gypsum and other evaporites being incorporated into the accumulating sediments.

The sediments of the Paraje Solo Formation consist of micaceous and ferrugenous (limonitic) clays, silts, fine- to medium-grained sandstones, organic debris (lignites), volcanic ash, and gypsum. This lithology is consistent with the low-lying, coastal, warm-temperate, brackish-water environments of modern mangrove peat accumulation generally, and the local volcanic supplements of the Coatzacoalcos region.

Samples were obtained from six exposures of the Paraje Solo Formation located SSE of Coatzacoalcos, Veracruz, Mexico (Fig. 2). Collections were made along the Ferrocarril del Sureste (sites 1, 2, 3) and from roadcuts along Mexico 180 (sites 4, 5, 6). The localities cover an area of approximately 20 km (between sites 2 and 4) by 8 km (between sites 3 and 5) at 18°20′N latitude and 95°N longitude.

SITE 1

This site was along a small bank on the W side of the railroad at km marker 34.4. The base of the section was a grey micaceous siltstone, with organic debris, measuring 0.6 m from the base to an overlying layer of highly organic (lignitic) siltstone. Sample 1 was obtained from the lower siltstone. Preservation was poor and fewer than 50 grains per slide were encountered. Thick-walled monolete fern spores were most abundant, and total spores constituted 65% of the sample (Table 1), possibly reflecting differential preservation.

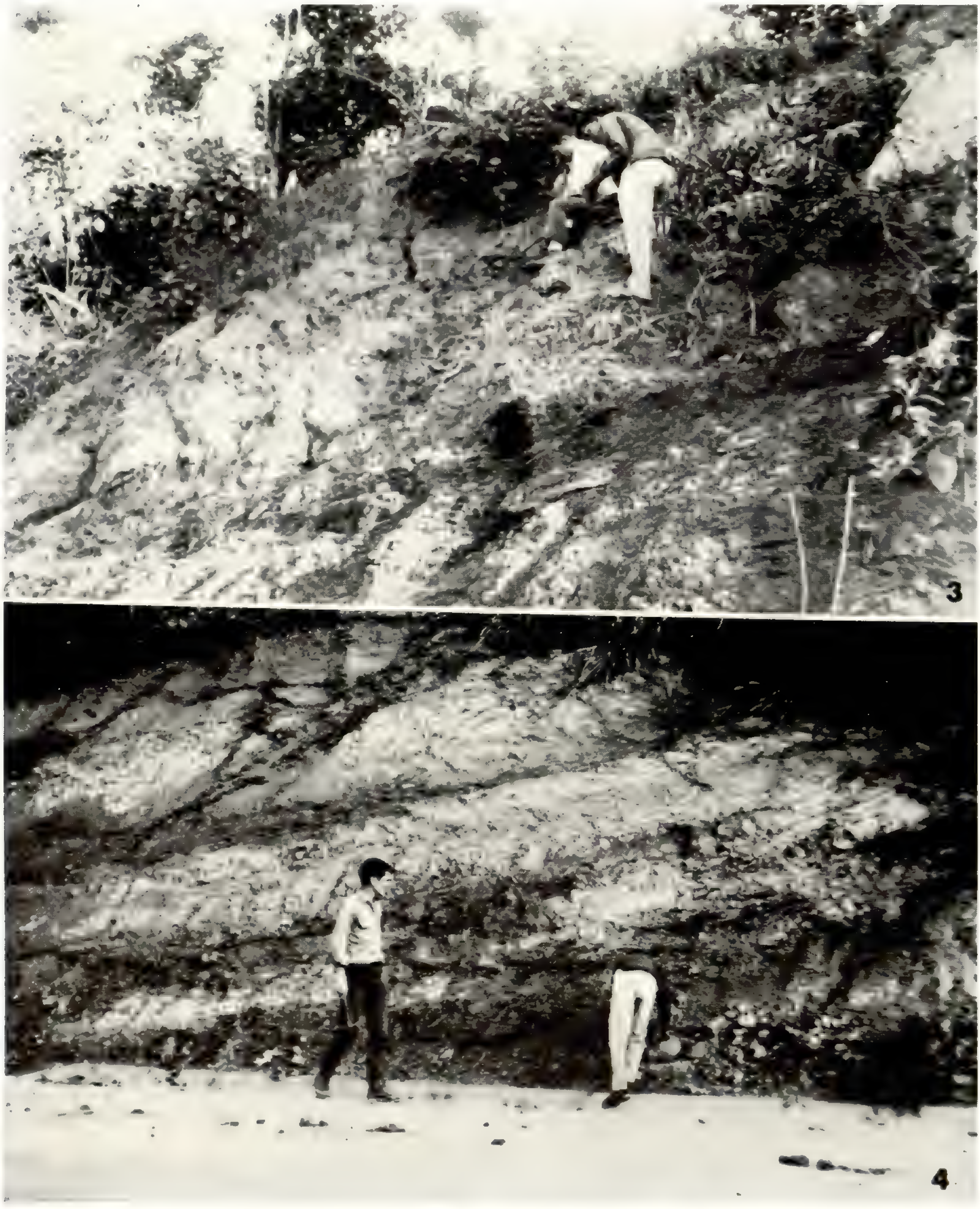
Above the siltstone was a lignitic siltstone 10 cm thick, containing well-preserved plant microfossils, from which sample 2 was obtained. Overlying the lignitic siltstone was a 10 cm layer of fine-grained sandstone. Sample 3 from this sandstone was barren. Above the sandstone was 8 cm of a conspicuous layered lignite (sample 4) and a good pollen and spore flora was recovered.

SITE 2 (Fig. 3)

This site is 1.6 km SE of site 1 at km marker 36. Sample 5 was collected from a basal grey mudstone and contained a greater diversity of palynomorphs than the approximate stratigraphically equivalent layer at site 1 (sample 1). Sample 6 was a grey muddy siltstone with quartz particles collected 15 cm above sample 5. Sample 7 was 15 cm above sample 6. Sample 8 was from the siltstone 25 cm above sample 7. Sample 9 was taken from the grey silstone. Sample 10 was taken from a buff-colored, muddy clay siltstone with higher organic content than samples 5–9 and with a more diverse microflora.

SITE 3

This site was a south-facing bluff at km marker 28, 5.6 km NW of site 1. The locality was at the settlement of Trancas Viejas, opposite the entrance to the Pemex locality Moloacan Noreste #2. Samples 11–16 were collected, but only numbers 13 and 15 contained pollen and spores. Sample 13 was a medium brown siltstone, highly organic, ferruginous and micaceous. Above sample 13 was a 10 cm layer of sandstone from which sample 14, barren of pollen and



FIGURES 3–4. Collecting localities for lignites in the upper Miocene Paraje Solo Formation, vicinity of Coatzacoalcos, Veracruz, Mexico. Field associates are Mr. David Jarzen and Mr. Enrique Martínez-Hernández (January 30, 1967).—3. Site 2.—4. Site 5.

spores was obtained. Above the sandstone was a 5 cm layer of a dark-brown silty lignite. Sample 15 was taken from the lignite.

SITE 4

Site 4 is approximately 8.5 km NNW of site 3, and about 16 km from sites 1 and 2. The localities are exposed along a roadcut of Mexico 180 on the S

side of the road. Samples 17–26 (bottom to top) were obtained at 30 cm intervals from a channel cut, and samples 28–33 from a parallel channel cut 6 m W along the same roadcut. From the first group, samples 17, 19, 21, and 25 contained plant microfossils, and from the second group, samples 30, 32, and 33. The lithology and stratigraphic relationships between these samples are given below:

East Channel Cut	6 m	*West Channel Cut*
Sample 25, light buff-colored, moderately organic siltstone		
Sample 21, dark brown lignitic siltstone		Sample 33, dark brown lignitic siltstone
		Sample 32, thin lignitic siltstone
Sample 19, brown lignitic siltstone		Sample 30, brown lignitic siltstone
Sample 17, light buff-colored moderately organic siltstone		

SITE 5 (Fig. 4)

This locality is 6 km E of site 4 on the N side of Mexico 180. The section consists of lignites and fine-grained lignitic siltstones. Samples 34–43 were collected, and 34, 35, 37, 38, and 40 contained plant microfossils. Sample 34 is a light-grey siltstone and sample 35 a light buff-colored siltstone with paper-thin layers of black organic material. Samples 37 and 38 were from the bottom and top, respectively, of a 30 cm thick highly organic lignitic siltstone. Sample 40 was from a grey siltstone. Three additional collections were made in the sandstone above (samples 41–43) but all were barren or contained only poorly preserved pollen and spores.

SITE 6

This locality is 1 km E of site 5 on the S side of Mexico highway 180. In 1967 the site was adjacent to a sign designating Pemex locality Teapa Nueva Ote No. 1. Samples 44–55 were collected, and 44, 45, 49, 51, and 54 contained pollen and spores. Samples 44 and 45 were buff colored highly organic lignitic siltstones from the bottom and top of a basal lignite, sample 49 was a lignite, and samples 51 and 54 were indurated, nearly coalified lignites with a scattered surficial layer of sulfur. Samples 44, 45, and 49 contained high percentages of *Quercus*, while numbers 51 and 54 contained 86% and 91% *Rhizophora*, respectively (Table 1).

Sediment deposition in mangrove environments is rapid, and no significant time interval is likely represented in the 5–6 m distance between the lowest

TABLE 2. Taxa represented by fossil pollen and spores in the Paraje Solo Formation, Veracruz, Mexico.

Psilopsida
Psilotum
Lycopsida
Lycopodium
Selaginella
Cyatheaceae
Alsophila
Cyathea
Hemitelia
Gleicheniaceae
Dicranopteris
Gymnogrammaceae
Pityrogramma
Lomariopsidaceae
Lomariopsis (*Stenochlaena*)
Parkeriaceae
Ceratopteris
Polypodiaceae
Monolete Fern Spores, types 1, 2, 3, 4, 5, 6
Pteris, types 1, 2, 3
Pinaceae
Abies
Picea
Pinus, types 1, 2
Podocarpaceae
Podocarpus
Araceae
Spathiphyllum
Cyperaceae
Dioscoreaceae
Rajania
Gramineae
Liliaceae
Smilax
Palmae
cf. *Astrocaryum*
cf. *Attalea*
cf. *Brahea*
cf. *Chamaedorea*
cf. *Maximiliana* type
Acanthaceae
Bravaisia
Justicia
Amaranthaceae
Iresine
Amaranthaceae-Chenopodiaceae
Anacardiaceae
Comocladia
Aquifoliaceae
Ilex
Betulaceae
Alnus
Boraginaceae
Tournefortia
Burseraceae
Bursera
Protium
Chloranthaceae
Hedyosmum
Combretaceae
Combretum/*Terminalia*
Laguncularia
Compositae, types 1, 2, 3, 4, 5, 6
Dichapetalaceae
Dichapetalum
Euphorbiaceae
Alchornea
cf. *Bernardia*
cf. *Sapium*
cf. *Stillingia*
cf. *Tetrorchidium*
cf. *Tithymalus*
Fagaceae
Quercus
Flacourtiaceae
Casearia
Laetia
Guttiferae
Symphonia
Hamamelidaceae
Liquidambar
Juglandaceae
Engelhardtia
Juglans
Lecythidaceae
Gustavia
Leguminosae
cf. *Acacia*
Desmanthus
Mimosa (cf. *M. pigra*)
Lentibulariaceae
Utricularia
Loranthaceae
Struthanthus
Lythraceae
Cuphea
Malpighiaceae
cf. *Hiraea*
cf. *Malpighia*
cf. *Mezia* (?) type
Malvaceae
Hampea, *Hibiscus*
Meliaceae
Cedrela
Guarea
Myricaceae
Myrica
Myrtaceae
Eugenia/*Myrcia*

TABLE 2. (Continued).

Onagraceae
Ludwigia
Passifloraceae
Passiflora
Polygalaceae
cf. *Bredemeyera*
cf. *Securidaca*
Polygonaceae
Coccoloba
Ranunculaceae
Thalictrum
Rhizophoraceae
Rhizophora
Rubiaceae
cf. *Alibertia*
Borreria
Faramea
Terebrania
Salicaceae
Populus
Sapindaceae
Allophylus
Cupania
Matayba
Meliosma
cf. *Paullinia* (e.g., *P. pinnata*)
cf. *Paullinia* (e.g., *P. turbacensis*)
Serjania
Sterculiaceae
Buettneria
Theaceae
Cleyera
Thymeliaceae
Daphnopsis
Ulmaceae
Celtis
Ulmus

and uppermost samples. The distribution of palynomorphs among the six sites (Table 1) does not reveal any clustering that can be related to specific stratigraphic levels or attributed to age differences between sites. The variations in pollen types and percentages more likely reflect habitat differences in this region of considerable topographic diversity. The fossil pollen and spores, therefore, are regarded as more or less contemporaneous elements of a single floral unit occupying southeastern Veracruz during a brief span of upper Miocene time.

THE MIOCENE COMMUNITIES

The reconstruction of upper Miocene vegetation in southern coastal Veracruz is based on 110 identified types of pollen and spores from the Paraje Solo Formation (Table 2), and these are arranged into paleocommunities as diagramed in Fig. 5 (see also Table 3). Along the left and lower sides of Fig. 5 are the modern communities recognized for Veracruz by Gómez-Pompa (1973) placed according to approximate altitudinal occurrences. The generic names represent fossil pollen and spores identified from the Paraje Solo Formation. Several genera (e.g., *Rhizophora*, *Liquidambar*, *Abies*) are characteristic of specific communities (e.g., Manglar, Deciduous Forest, Needle-Leaved Forest) and these identify the principal types of associations present during the upper Miocene. Other genera range widely throughout several communities (e.g., *Alchornea*, cf. *Sapium*) and are placed in Fig. 3 according to all known principal occurrences. Three east-west transects are shown illustrating variations in the ca. 1,600 m to coastal zone vegetation in Veracruz.

Paramo vegetation presently occurs at the highest altitudes and is characterized by composites (*Cnicus*, *Gnaphalium*, *Senecio*), grasses (*Festuca*, *Muhlenbergia*, *Stipa*), and various other genera including *Asplenium* and *Draba*.

TABLE 3. Taxa of fossil pollen and spores from the Paraje Solo Formation arranged into paleocommunities, based on the composition of modern vegetation types in Veracruz. Fossil pollen of the Compositae, Cyperaceae, and Gramineae, undifferentiated generically, is present and ranges throughout most present-day communities.

Needle-Leaved and Scale-Leaved Forest (including pine and pine-oak forests):
Abies, *Picea*, *Pinus*, *Alchornea*, *Alnus*, *Quercus*, cf. *Sapium*, *Coccoloba*, *Smilax*, cf. *Stillingia*
Cyathea (in atypically low-altitude *Pinus strobus* forest near Tlapacoyan, 500 m; mixture of high selva and deciduous forest elements)
Liquidambar, *Myrica* (in atypically low-altitude *Pinus oocarpa* forest on the eastern slopes of Volcán Santa Marta, 500 m; mixture of lowland and deciduous forest elements)

Broad-Leaved (oak) Forest:
Alchornea, *Coccoloba*, *Quercus*, cf. *Sapium*

Deciduous (oak-*Liquidambar*) Forest:
Psilotum, *Lycopodium*, *Selaginella*, *Alsophila*, *Cyathea*, *Pinus*, *Podocarpus*, *Alchornea*, *Alnus*, cf. *Chamaedorea*, *Cleyera*, *Dichapetalum*, *Engelhardtia*, *Eugenia*, *Guarea*, *Hampea*, *Hedyosmum*, *Ilex*, *Iresine*, *Juglans*, *Justicia* (widespread), *Liquidambar*, *Meliosma*, *Myrica*, *Populus* (riparian, widespread), *Quercus*, *Struthanthus*, *Tournefortia*, *Ulmus*

High Evergreen Selva:
Lycopodium, *Podocarpus*, *Alchornea*, *Allophylus* (secondary), cf. *Astrocaryum*, *Bursera*, *Casearia*, *Cedrela*, cf. *Chamaedorea*, *Cupania*, *Faramea*, *Guarea*, *Gustavia*, *Hampea*, *Hibiscus*, cf. *Hiraea*, *Iresine*, *Matayba*, *Myrcia*, cf. *Paullinia*, cf. *Sapium*, *Spathiphyllum*, *Symphonia*, *Terminalia*, cf. *Tetrorchidium*

High Semi-Evergreen Selva:
Lycopodium, *Selaginella*, *Cyathea*, *Alchornea*, cf. *Bernardia* (secondary), *Bursera*, *Casearia*, *Cedrela*, cf. *Chamaedorea*, *Cupania*, *Daphnopsis*, *Faramea*, *Hampea*, *Hibiscus*, *Ilex*, *Iresine*, cf. *Paullinia*, *Protium*, *Quercus*, *Rajania*, cf. *Sapium*, *Securidaca* (secondary), *Spathiphyllum*, cf. *Tetrorchidium*, *Ulmus*

Low Evergreen Selva:
Ilex, *Myrica*

Low Semi-Evergreen Selva:
cf. *Acacia*, *Coccoloba*, *Eugenia*

Low Deciduous Selva:
cf. *Acacia*, cf. *Brahea*, *Bursera*, *Casearia*, *Celtis*, *Combretum*, *Cupania*, *Daphnopsis*, *Eugenia*, *Ilex*, cf. *Sapium*, *Comocladia*

Low Thorn Selva:
cf. *Acacia*, *Eugenia*, *Laetia*, cf. *Malpighia*, *Mimosa*

Palm Stands:
Coccoloba, *Cupania*, *Desmanthus* (secondary), Palmae, *Quercus*

Savanna:
Coccoloba, Gramineae, *Hibiscus*, *Mimosa*, *Myrica*, *Quercus*

Temperate Grassland:
Selaginella, Gramineae, *Quercus*

Saline Grassland:
Gramineae

Nolina-Hechtia-Agave Desert:
None

Thorn Scrub:
cf. *Acacia*, *Bursera*, *Quercus*

TABLE 3. (Continued).

Swamp/Aquatic Vegetation:
Ceratopteris, Bravaisia, Ludwigia

Mangrove Swamps:
Hibiscus, Laguncularia, Ludwigia, Mimosa (*M. pigra* type), *Rhizophora,* cf. *Sapium, Utricularia*

Paramo Vegetation:
None

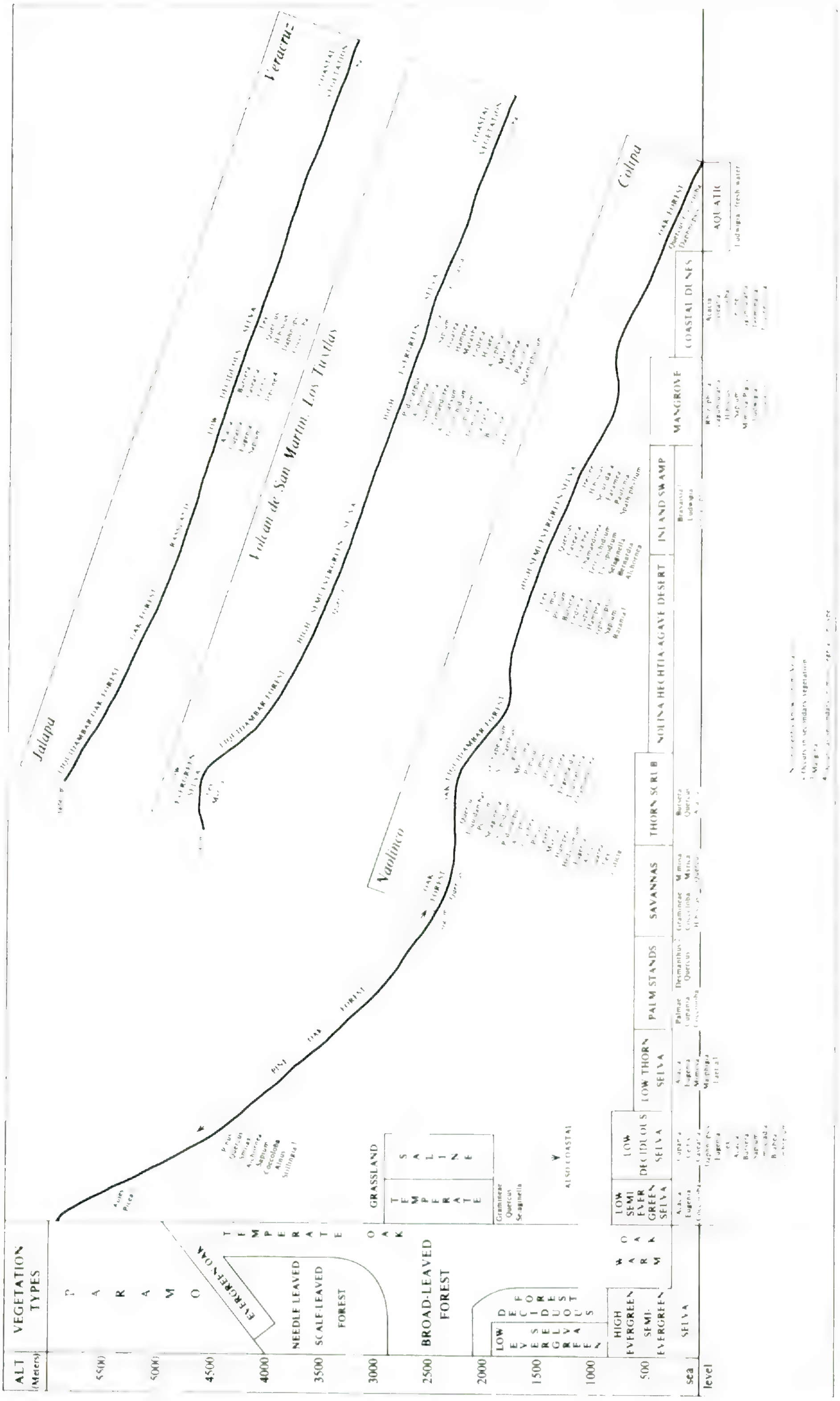
Coastal Dune Vegetation:
cf. *Acacia, Casearia, Coccoloba, Iresine, Laguncularia, Terminalia, Tournefortia*

Genera occurring in secondary vegetation:
Alibertia, Allophylus, Alnus, cf. *Acacia, Borreria, Buettneria, Combretum, Casearia, Cuphea, Cedrela, Desmanthus, Eugenia, Hibiscus, Iresine, Mimosa, Passiflora, Securidaca, Serjania, Smilax, Tournefortia*

Since the common plants of Paramo vegetation belong to stenopalynous groups, and grow removed from the depositional basin, it is not possible to assess the presence of this community on palynological evidence. As noted earlier, however, there is no reason to assume the absence of the Paramo during the upper Miocene since highlands have been available in eastern Mexico since post-Cretaceous times.

Pollen of *Abies* in the Paraje Solo microflora documents the presence of the Needle-Leaved Forest among Miocene communities of Veracruz. Pollen of *Pinus* and *Quercus* is also represented, and these are dominant elements of the pine and pine-oak forests characteristic of high elevations in Mexico. In addition to the dominants, pollen of wider-ranging genera frequently associated with the Needle-Leaved Forest was recovered including *Smilax, Alchornea,* cf. *Sapium, Coccoloba,* and *Alnus.* The genus *Stillingia* is not presently known from Veracruz, but elsewhere it is associated with pine-oak forests. Several grains of *Picea* were found in 5 samples distributed among 3 sites (Table 1). Thus spruce was a significant member of the coniferous forest of Veracruz during the upper Miocene. The genus no longer occurs in Veracruz, and is represented in Mexico today only by *P. mexicana* Martínez (Coahuila, Nuevo León) and *P. chihuahuana* Martínez (Chihuahua, Durango; Gordon, 1968). The dominant member of the Scale-Leaved Forest, *Juniperus deppeana* Steud., and the commonly associated *Nolina* and *Sophora,* have not been identified in the microflora. Thus among the Needle-Leaved Forests there is evidence for the cool moist Bosque de Oyamel (*Abies, Picea*), Bosque de Pino (*Pinus*), and Bosque de Pino-Encino (*Pinus, Quercus*), but little evidence of the drier and warmer Bosque de Cedro y Táscate (*Juniperus, Nolina, Sophora*).

The Broad-Leaved Forests are oak communities of high elevations (evergreen oak), moderate elevations (temperate oak), and low elevations (warm oak). Each community is characterized by particular species of *Quercus* and associated genera. Since these species of oak cannot be distinguished on the basis of pollen characters, it is not possible to record precisely the type of Broad-


Veracruz
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Jalapa
Volcan de San Martin, Las Tuxtlas
Catemaco
Coatzacoalcos
Minatitlan
Acayucan
Tuxtepec
Oaxaca
Tehuantepec
Tapachula
Tuxtla Gutierrez
Comitan
Huehuetenango
Quetzaltenango
Totonicapan
Solola
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Escuintla
Retalhuleu
Mazatenango
Suchitepequez
Chimaltenango
Antigua
Chiquimula
Zacapa
Puerto Barrios
Coban
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Salama
Peten
Flores
Sayaxche
Tikal
Uaxactun
Belize
Chetumal
Merida
Campeche
Ciudad del Carmen
Villahermosa
Frontera
Tampico
Ciudad Victoria
Linares
Monterrey
Saltillo
Monclova
Piedras Negras
Nuevo Laredo
Matamoros
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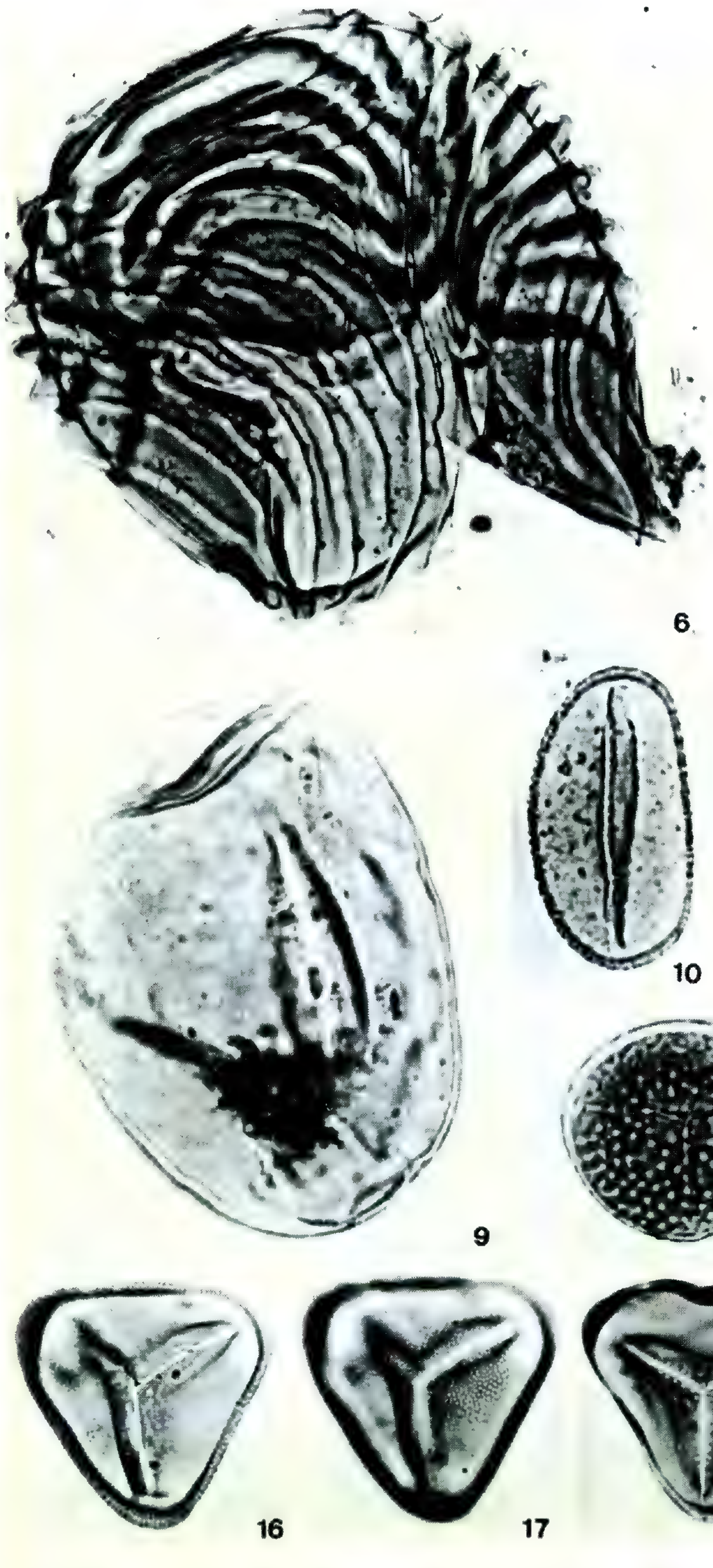
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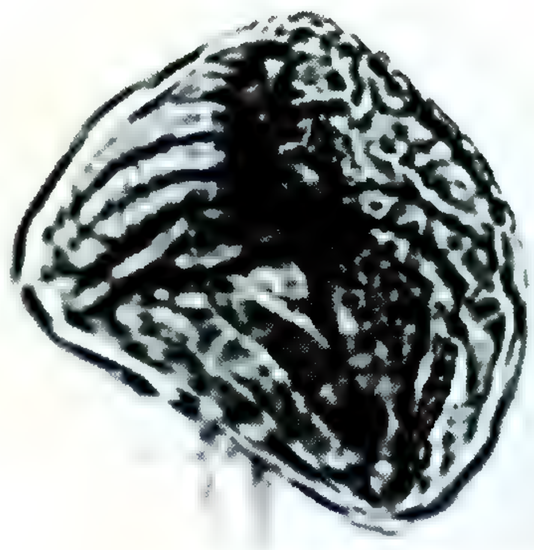
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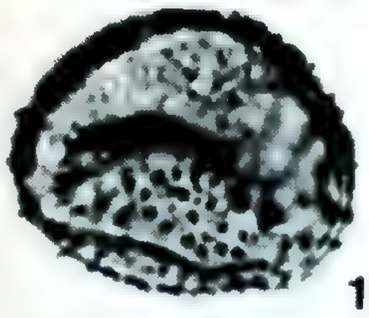
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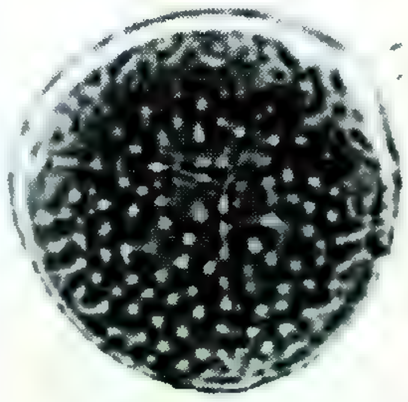
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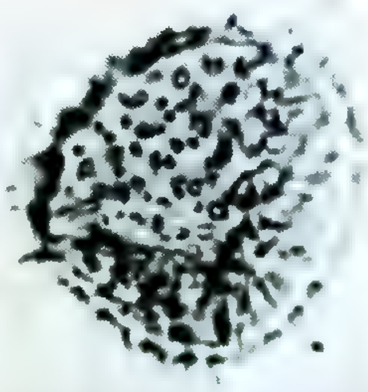
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FIGURES 6–19.—6. *Ceratopteris*, 44-1, V-30, 125 μ.—7–8. *Pityrogramma*, 5-1, C-12, 45 μ.—9. *Lomariopsis* (*Stenochlaena*), 8-1, U-32, 72 × 52 μ.—10. *Dicranopteris*, 19-1, E-11,1, 50 × 29 μ.—11. *Psilotum*, 37-1, K-12,2-4, 36 × 18 μ.—12–13, 15. *Selaginella*.—12. 10-1, Q-39,1, 36 μ.—13. 40-1, N-21,1-3, 32 μ.—15. 10-1, B-44,1, 38 μ.—14. *Lycopodium*, 38-1, P-18,1-3, 37 μ.—16–18. *Alsophila*.—16–17. 2-1, S-30, 50 μ.—18. 34-1, 0-14,1, 41 μ.—19. *Cyathea*, 13-1, T-36,2, 41 μ. [The numbers following plant names represent sample and slide number (e.g., 44-1), England Slide Finder coordinates (e.g., V-30), and size (e.g., 125 μ).]

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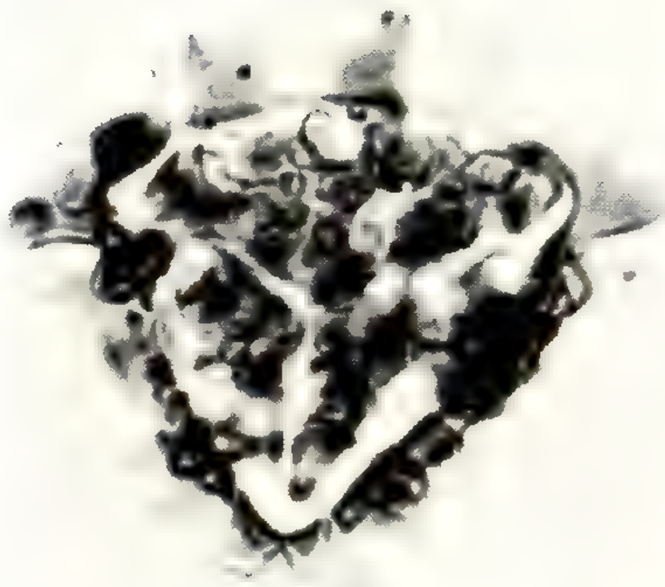

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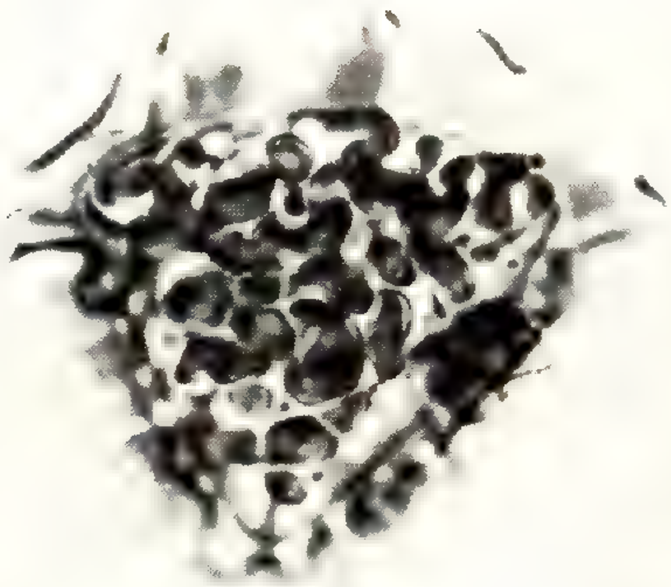

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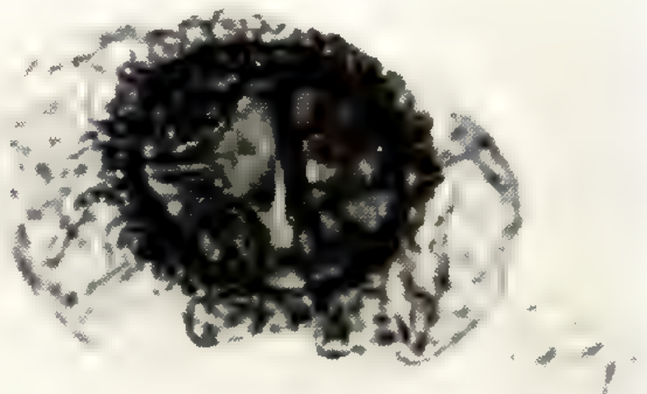

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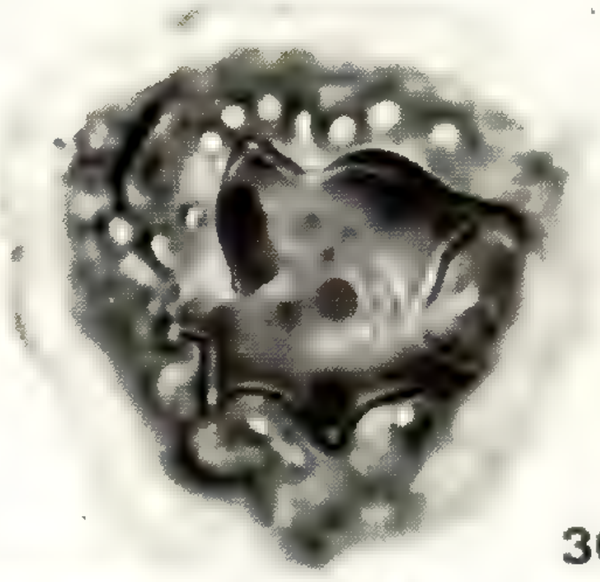

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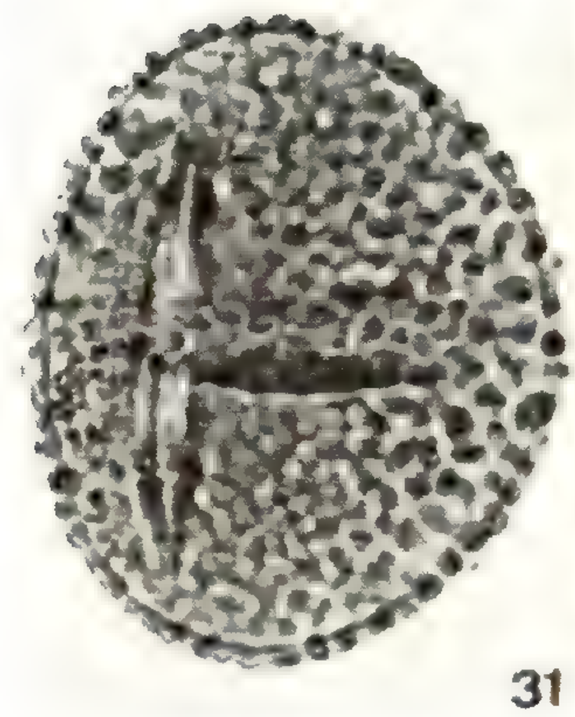

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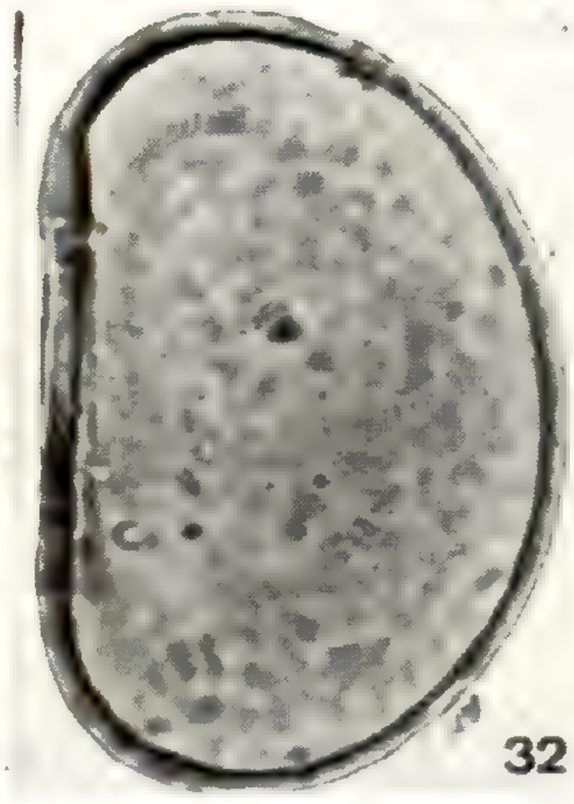

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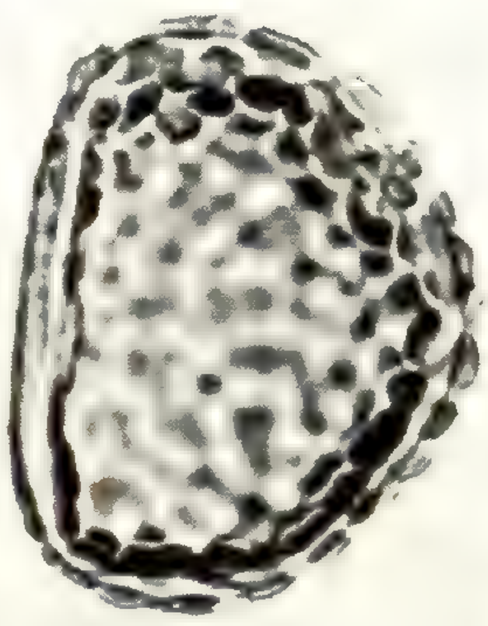

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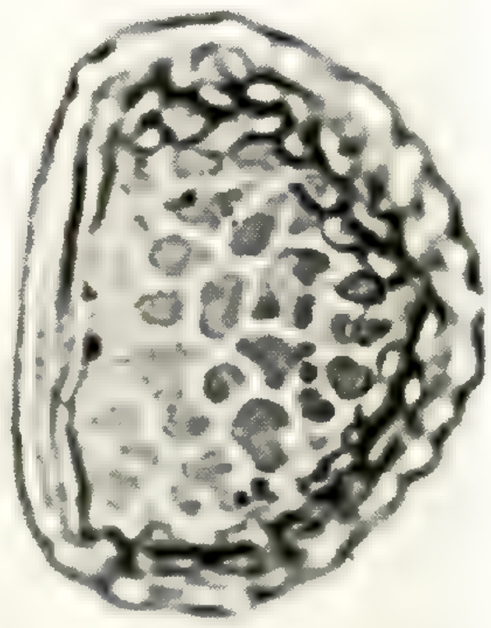

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FIGURES 20–34.—20–21, 25–26, 29–30. *Pteris*.—20–21. Type 1, 10-1, Q-25,3, 63 μ.—25–26. Type 2, 13-1, N-41,1, 59 μ.—29–30. Type 3, 25-1, D-29, 54 μ.—22, 31–34. Polypodiaceae.—22. Type 4, 30-1, V-26,1, 49 × 39 μ.—31. Type 3, 25-1, K-48,2-4, 56 × 48 μ.—32. Type 1, 32-1, X-42,2, 69 μ.—33–34. Type 2, 13-1, R-22,4, 54 × 41 μ.—23–24. *Hemitelia*. 23. Type 1, 35-1, Q-48,2, 32 μ.—24. Type 2, 1-1, M-48, 37 μ.—27–28. *Podocarpus*. 25-1, R-41,3, 31 × 22 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

TABLE 4. Synopsis of genera and distributional ranges of taxa represented by fossil pollen and spores in the Paraje Solo Formation, but presently unreported for the modern flora of Veracruz. Tentative identifications (e.g., cf. *Brahea*) are not included. *Symphonia*, unverified for the modern flora at the beginning of the study, has recently been reported from the High Evergreen Selva (Gómez-Pompa, pers. comm., 1974).

Ceratopteris	A floating fern of Tabasco, Central America (Guatemala, Honduras, El Salvador, Costa Rica, Panama), and the Greater Antilles (Cuba, Haiti, Dominican Republic, Puerto Ricó).
Picea	Highlands of northern Mexico; *P. chihuahuana* (Chihuahua, Durango) and *P. mexicana* (Coahuila, Nuevo León).
Gustavia	Costa Rica, Panama, and south (Colombia, Venezuela, the Guianas, Brazil, Peru).
Laetia	Campeche, Tabasco, Yucatán, Chiapas, Quintana Roo, Central America (British Honduras, Guatemala, Panama), and the Antilles (Cuba, Andros in the Bahamas, Dominican Republic, Jamaica, Martinique).
Rajania	A West Indian segregate of *Dioscorea*; Cuba, Hispaniola, Jamaica, Puerto Rico.

Leaved Forest present in Veracruz during the Miocene. Fossil pollen of *Quercus* is present at all sites, however, and at site 6 reaches 34% of the microflora. Since no members of the high (e.g., *Abies, Picea, Pinus*) or middle (e.g., *Liquidambar*) altitude communities reach such high percentages, it is likely that site 6 records the presence of a lowland oak assemblage, possibly of *Q. oleoides* Cham. & Schlecht.

The Deciduous Forest south of Misantla consists of *Liquidambar macrophylla* Oerst. and several species of oak, including *Q. affinis* Schwidw. as dominants. In the Sierra de Los Tuxtlas the dominants are *L. macrophylla, Q. skinneri* Benth., *Ulmus mexicana* Liebm., and *Meliosma alba* (Schlecht.) Walp. (Sousa, 1968). Pollen of all these genera occur in the Paraje Solo Formation. In addition, pollen of a number of genera commonly associated with the oak-*Liquidambar* forest are also present (Fig. 5). The Deciduous Forest is one of the principal associations represented in the microflora, in contrast to the selvas, remnants of which presently occupy much of the Veracruz lowland.

Selvas are not well represented in the Paraje Solo microflora considering the diversity of genera and lowland habitat of these communities. The High Evergreen Selva of Veracruz includes *Terminalia amazonica* (Gmel.) Exell, *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoullia flammea* Oliver, *Brosimum alicastrum* Swartz, *Ficus tecolutensis* (Liebm.) Miq., and *Pseudolmedia oxyphyllaria* Donnell Smith as frequent multi-dominants. Among these *Terminalia* pollen is tentatively recorded, but these grains are similar to *Combretum*. One species (*T. catappa* L.) grows outside the selvas in Coastal Dune and Island Vegetation (Gómez-Pompa, 1973: 139–143), but it is considered introduced. Common associates of the High Evergreen Selva recorded in the microflora are frequently genera found in other communities, such as *Podocarpus* and *Guarea* in the Deciduous Forest, species of *Bursera* in the Thorn Scrub and Low Deciduous Selva, and *Alchornea* and cf. *Sapium* widespread through several associations. A few genera most commonly found

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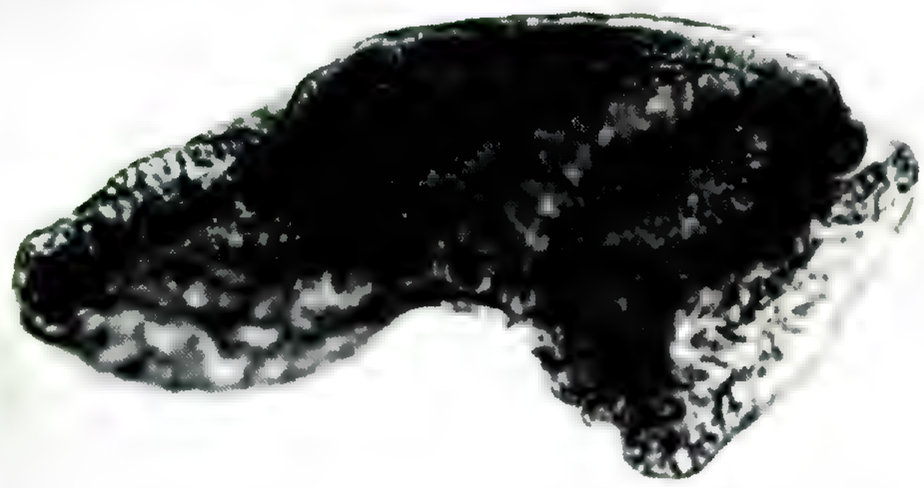

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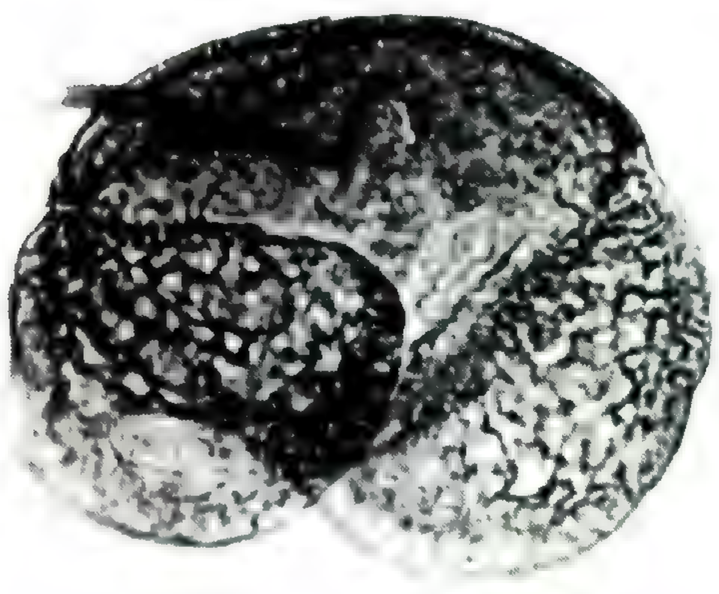

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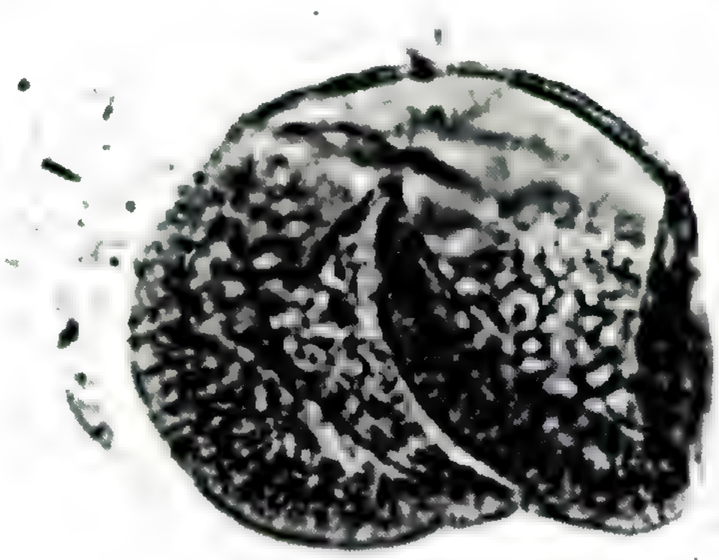

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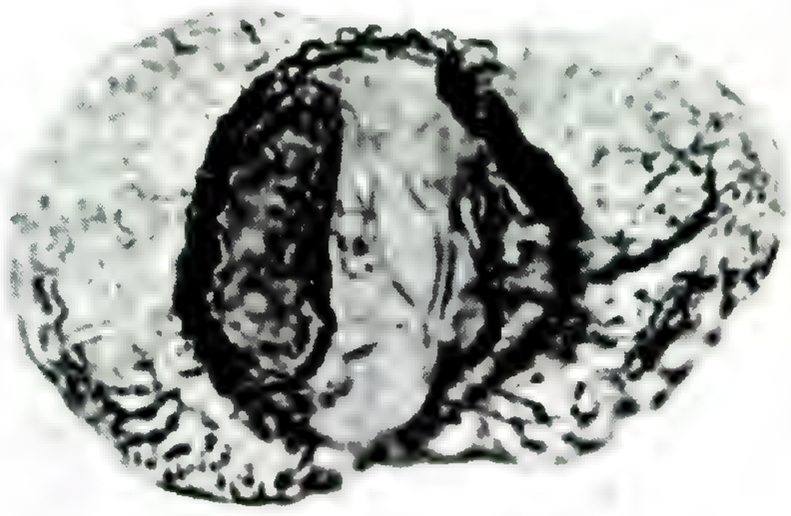

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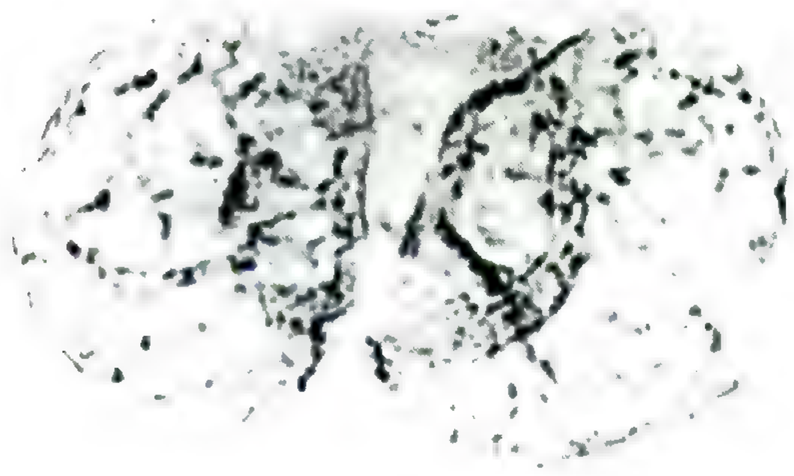

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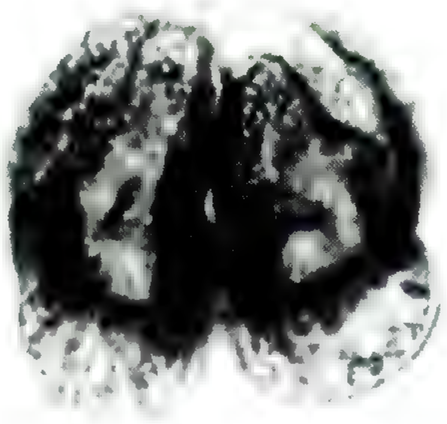

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Figures 35–43.—35–36. Polypodiaceae.—35. Type 5, 10-1, 0-41,3, 53 × 36 μ.—36. Type 6, 13-1, X-36,3, 47 × 36 μ.—37. *Abies*, 2-1, E-20,2-4, 110 × 40 μ.—38–39. *Picea*.—38. 5-1, L-42,1-3, 72 × 50 μ.—39. 37-1, B-24,1, 63 × 45 μ.—40, 43. *Pinus*.—40. Type 1, 21-1, L-16, 98 × 60 μ.—43. Type 2, 4-1, P-35,1, 45 × 36 μ.—41–42. *Podocarpus*.—41. 40-1, P-17,1, 72 × 47 μ.—42. 9-1, S-48,2, 76 × 47 μ. [The numbers following plant names represent sample and number, England Slide Finder coordinates, and size.]

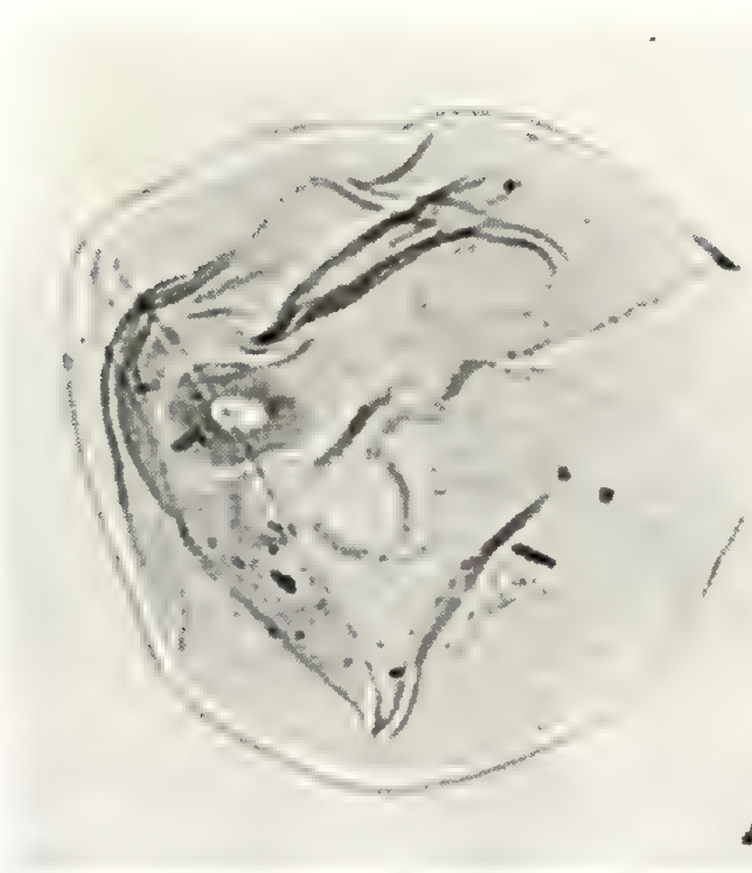
in the High Evergreen Selva are present in the microflora (e.g., *Hiraea*, *Myrcia*). However, considering the near absence of the dominants and infrequent occurrence of equivocal associates, the High Evergreen Selva appears to have been less well-defined and of more restricted distribution during the upper Miocene than at present. The same is true for the related High Semi-Evergreen and Medium Semi-Evergreen selvas (Fig. 5).

The remainder of the selvas grow in environments of reduced rainfall (e.g., to the lee of local highlands) or under edaphic conditions (poor, coarse soil) resulting in moisture stress. This category of drier to arid communities is poorly represented in the Paraje Solo microflora. Among genera found in the Low Evergreen Selva only the wide-ranging *Ilex* and *Myrica* were recovered. None of the characteristic genera of the Low Semi-Evergreen Selva are presently known from the fossil assemblage, with the possible exception of *Coccoloba* which is found in other types of vegetation. None of the dominants of the Low Deciduous Selva have been found, but this community is represented by some common associates (cf. *Acacia*, cf. *Brahea*, *Bursera*, *Casearia*, *Celtis*, *Combretum*, *Comocladia*, *Cupania*, *Daphnopsis*, *Eugenia*, *Ilex*, and cf. *Sapium*). Similarly the Low Thorn Selva is represented by cf. *Acacia*, *Eugenia*, cf. *Malpighia*, *Mimosa*, and *Laetia* (presently unknown from Veracruz; Table 4). Some of these range into more mesic communities (e.g., *Eugenia* in the Deciduous Forest), and it is probably significant that the fossil pollen of cf. *Acacia* appears most similar to *A. farnesiana* (L.) Willd. and *Mimosa* to *M. pigra* L. These two species have relatively broad ecological tolerances and extend into more humid environments than is usual for the respective genera.

Progressing to more xeric and distinctly arid vegetation types, not only the dominants but almost all important associated genera are absent from the Paraje Solo microflora. This includes the *Nolina-Hechtia-Agave* Desert and the Thorn Scrub. Among genera listed for the former by Gómez-Pompa (1973: 135–137) none are represented, and from the latter, pollen of only *Bursera*, cf. *Acacia* and *Quercus* is present. Although individual elements of a subhumid vegetation are represented in the fossil assemblage, there is little evidence they were aggregated into definite communities of wide distribution in southeastern Veracruz.

The occurrence of two communities in Veracruz, the Palm Stands and Savannas, are of interest because of possible anthropogenic influences necessary for their genesis and persistence. Three genera of palms occur as stands in Veracruz, *Scheelea*, *Sabal*, and *Paurotis*. Pollen of these has not been recovered, and the amounts of six other palm types do not suggest stands of palms (Table 1), but rather scattered occurrence as elements in other vegetation types. Although these results are not directly related to the problem of origin of palm stands in Veracruz, it is likely, considering the lowland distribution of the plants, that *Scheelea*, *Sabal*, and *Paurotis* stands are at least of post upper Miocene development in south coastal Veracruz.

The problem of savannas is more difficult. The various genera of grasses, occurring in almost all kinds of communities, cannot be distinguished in the microflora. Also the number of nongrass genera consistently associated with the savanna in Veracruz (e.g., *Curatella americana* L.) is few, and therefore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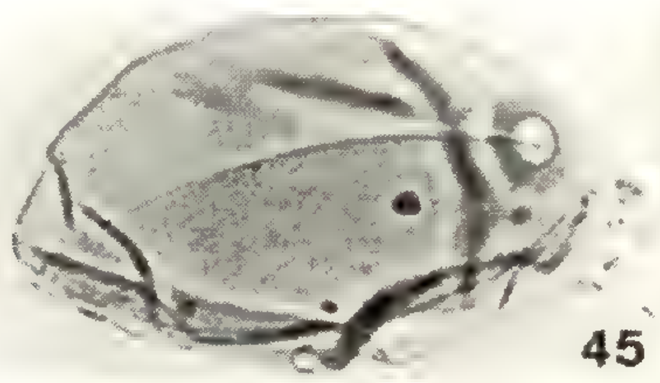
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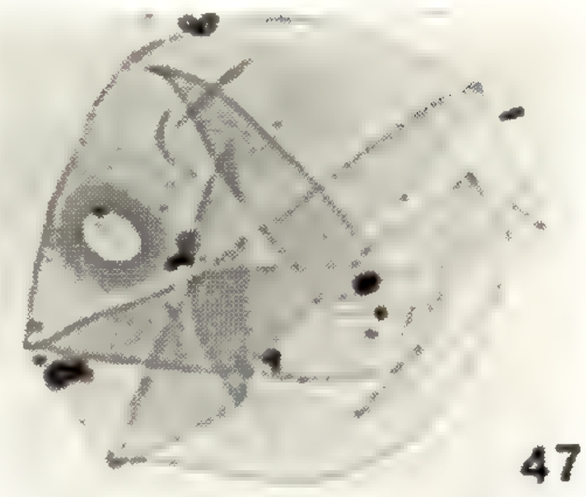
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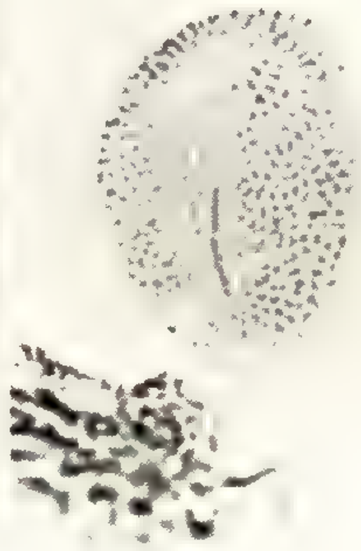
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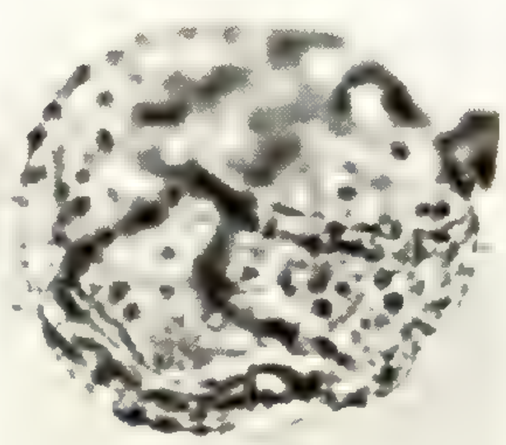
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FIGURES 44–60.—44–47. Gramineae.—44. 10-1, W-41,3, 63 μ.—45. 2-1, Y-45,1, 50 μ.—46. 2-1, R-30,1, 36 μ.—47. 13-1, Y-12,2, 50 μ.—48–50. *Spathiphyllum*.—48. 8-1, P-49, 35 × 22 μ.—49–50. 34-1, Q-36,3, 29 × 20 μ.—51. Cf. *Brahea*, 1-1, G-22,4, 40 × 20 μ.—52, 56. Cyperaceae.—52. 21-1, S-46, 58 μ.—56. 30-1, P-32,2, 49 μ.—53. Cf. *Astrocaryum*, 40-1, L-10,2, 68 × 44 μ.—54. Cf. *Maximiliana*, 2-1, K-29, 60 × 45 μ.—55. Cf. *Chamaedorea*, 4-1, D-31,4, 32 × 23 μ.—57–58. *Smilax*, 4-1, W-34,4, 41 μ.—59–60. Cf. *Attalea*.—59. 45-1, X-43,4, 45 × 32 μ.—60. 45-1, Q-11,1-2, 54 × 36 μ. [The numbers following plant names represent sample and number, England Slide Finder coordinates, and size.]

absence of this pollen in the microflora may not be significant. Considering savanna plants from Veracruz (Gómez-Pompa, 1973: 128–132) and Chiapas (Breedlove, 1973: 159–160) only *Hibiscus*, *Mimosa*, and *Myrica*, together with the grasses, possibly reflect the presence of savannas, and these genera are not diagnostic for the savannas. On the basis of limited evidence it appears more likely that Temperate and Saline grasslands account for the high percentage of grass pollen (maximum 45%) at site 4 (Table 1).

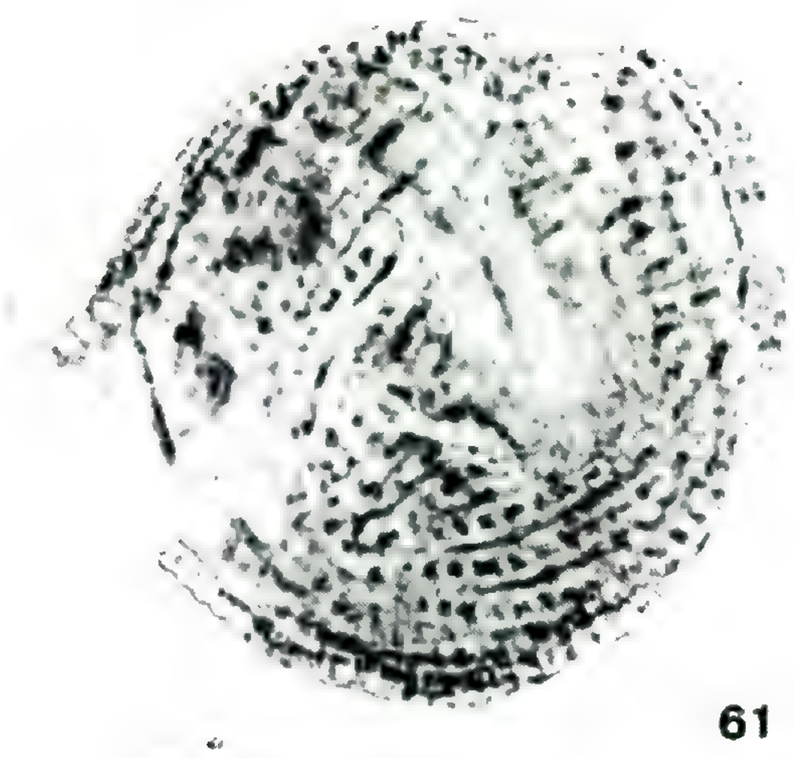
The most common pollen type in the Paraje Solo microflora is *Rhizophora* (maximum 96%, site 5). This is the dominant genus along the outer fringes of modern Manglar vegetation, with *Avicennia*, *Conocarpus*, and *Laguncularia* growing further inland. Pollen of *Laguncularia* is also abundant in the Paraje Solo Formation, especially at sites 3, 4, and 5. Elements from related swamp vegetation dominated by *Pachira aquatica* Aubl., found in waters of very slight salinity, also are present in the fossil assemblage. These include *Hibiscus*, *Laguncularia*, *Rhizophora*, and cf. *Sapium*. The large amounts of *Rhizophora* and *Laguncularia* pollen, with several associated genera, document Manglar as an important community in the upper Miocene vegetation of southern Veracruz.

Sedge pollen is found in the microflora in small amounts. The grains are thin-walled and frequently folded. Since the wedge shape is a characteristic feature of sedge pollen, percentages reported are usually minimum values. The Inland Swamps of Veracruz are characterized by the Cyperaceae together with other plants such as *Thalia geniculata* L. and *Pontederia sagitatta* Presl. Fossil pollen of *Thalia* and *Pontederia* has not been found and direct evidence for the presence of Inland Swamps is equivocal, but there is little reason to assume the absence of this community within a documented lowland environment.

Evidence for Coastal Dune vegetation near Coatzacoalcos during the upper Miocene is substantial. Pollen of cf. *Acacia*, *Casearia*, *Coccoloba*, *Iresine*, *Laguncularia*, *Terminalia*, *Tournefortia*, and numerous composites, grasses, and chenoams is common and all are members of this community (Gómez-Pompa, 1973: 139–143). For reasons to be considered in the discussion on paleoenvironments, it is likely that elements present in the microflora reflecting subhumid environments belong to the edaphically dry Coastal Dunes and Island Vegetation, and possibly to a Low Deciduous Selva type community occupying areas of physiographically controlled reduced rainfall (e.g., to the lee of the Sierra de Los Tuxtlas). There is little evidence of extensive climatically dry selvas, Thorn Scrub, and Deserts.

Pollen of Aquatic Vegetation has not been identified in the microflora, but for reasons noted earlier, this community is frequently underrepresented in lignites. Aquatic Vegetation is often of scattered and restricted distribution, pollen production is low, exines are occasionally poorly developed, and many belong to stenopalynous Gramineae, Cyperaceae, and Compositae (as marginal fringe vegetation). As with the Paramo and Inland Swamps, there is no climatic, physiographic, or stratigraphic (age) evidence suggesting these communities would be inappropriate to the upper Miocene landscape of Veracruz.

In summary, several communities of the modern flora of Veracruz are evident in the upper Miocene by pollen of characteristic dominant and associated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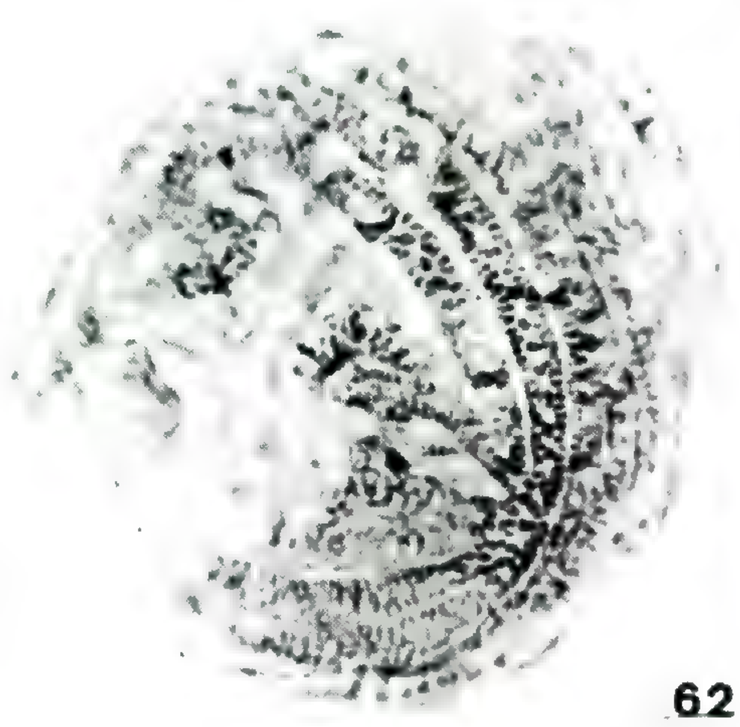
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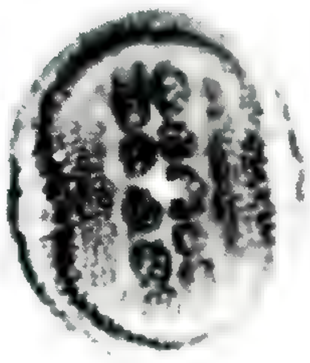
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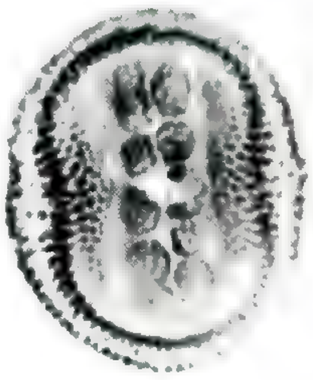
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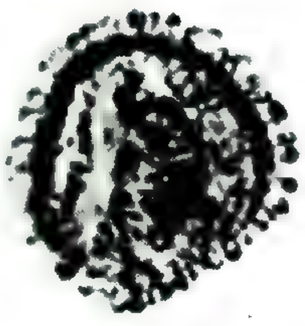
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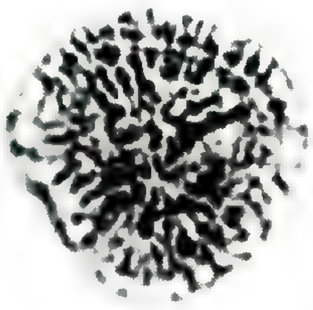
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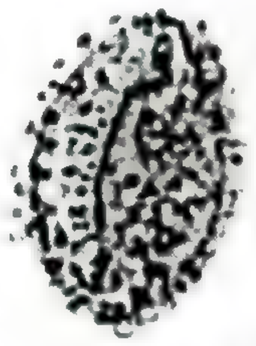
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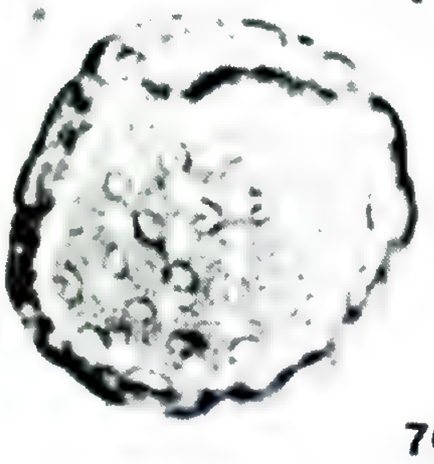
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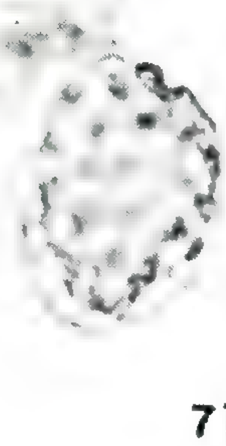
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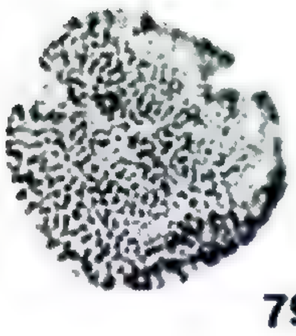
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FIGURES 61–85.—61–62. *Bravaisia*, 34-1, 0-33,2, 58 μ.—63–64. *Bursera*.—63. 2-1, K-18,4, 34 μ.—64. 40-1, U-12, 26 μ.—65–68. *Justicia*.—65–66. 30-1, L-21,1, 56 × 36 μ.—67–68. 2-1, E-16,1, 45 × 36 μ.—69–70. *Comocladia*, 35-1, R-30,2, 28 μ.—71–73. *Ilex*.—71–72. 10-1, E-14,2-4, 33 μ.—73. 35-1, R-17,1, 45 × 32 μ.—74. *Protium*, 1-1, Y-23,1, 33 × 21 μ.—75. *Tournefortia*, 13-1, W-20, 29 × 31 μ.—76–78. Amaranthaceae-Chenopodiaceae.—76. 21-1, E-17, 41 μ.—77–78. 10-1, H-30,3-4, 26 μ.—79. *Hedyosum*, 13-1, R-47,2-4, 30 μ.—80. *Iresine*, 8-1, Y-23,1, 18 μ.—81–82. *Alnus*, 38-1, M-31, 23 μ.—83. *Dichapetalum*, 25-1, D-10,2-4, 15 μ.—84–85. *Alchornea*.—84. 10-1, T-18,1, 23 μ.—85. 9-1, G-41,2-4, 24 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

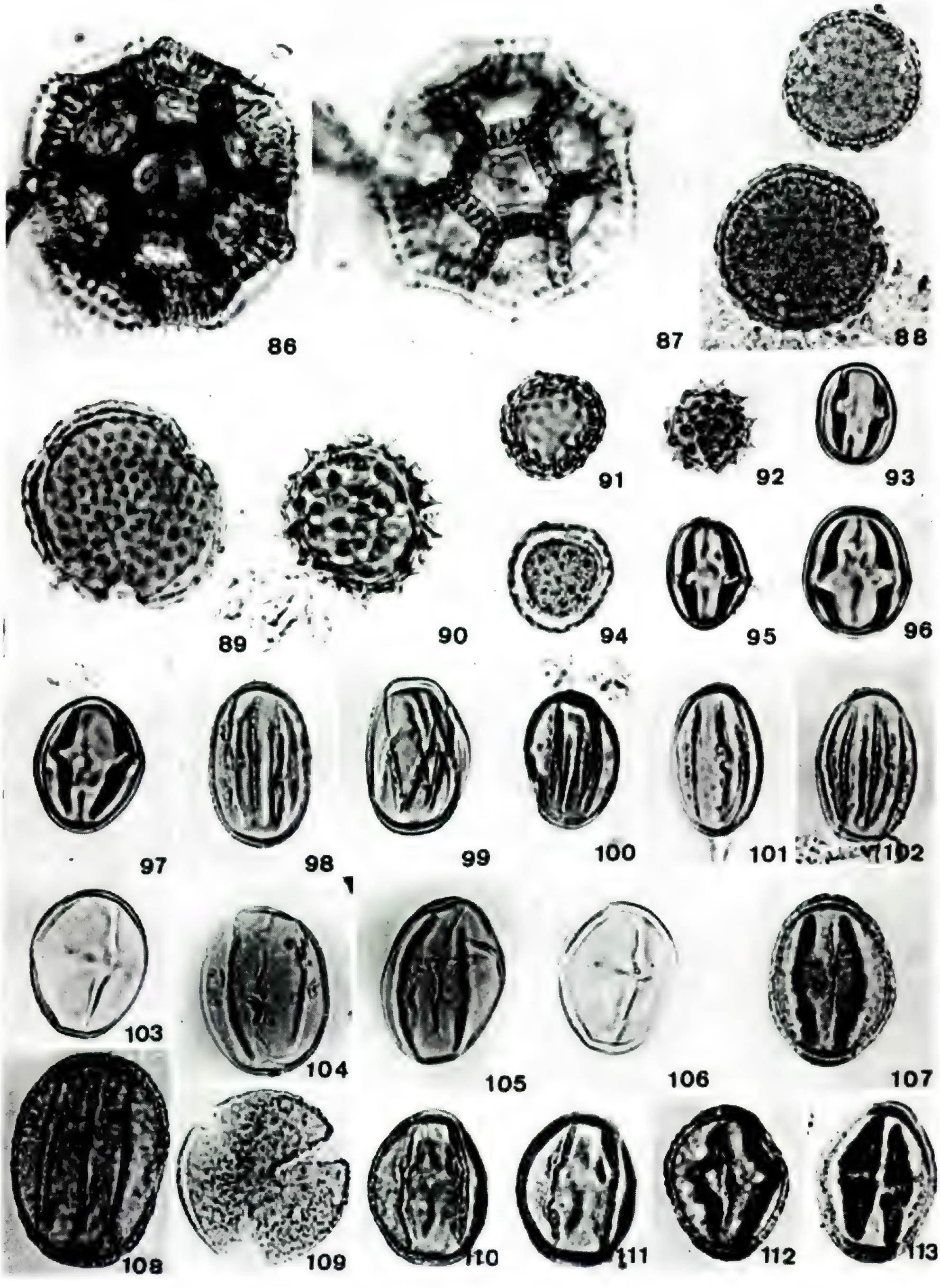
genera. These include the Needle-Leaved Forests of Bosque de Oyamel, Bosque de Pino, and Bosque de Pino-Encino; the Broad-Leaved Forests of warm, and probably temperate and evergreen oak communities; the Deciduous Forest; Temperate and Saline Grasslands; Mangrove Swamps; Coastal Dune Vegetation; and possibly a restricted and modified Low Deciduous Selva type of community. Some other types of vegetation, underrepresented for various reasons, were likely present. These are the Paramo, Inland Swamps, and Aquatic Vegetation. Absent or poorly represented vegetation types are the Scale-Leaved Forests (Bosque de Cedro y Táscate); High Evergreen Selva; High Semi-Evergreen Selva; Medium Semi-Evergreen Selva; Low Evergreen Selva; Low Semi-Evergreen Selva; Low Thorn Selva; Palm Stands; Savannas; *Nolina-Hechtia-Agave* Desert; and Thorn Scrub.

MEGAFOSSILS

Only a single paper describes a substantial megafossil flora from Tertiary deposits in Mexico (Berry, 1923). The specimens are from two presumed Miocene localities in southern Mexico. One is in the state of Oaxaca near Palomares, along Mexico 185 about mid-way between Matías Romero and the Oaxaca-Veracruz border. The flora consists of *Acrostichum mexicanum* Berry, *Gymnogramme wadii* Berry [*Gymnocladus wadii* (Berry) Maldonado-Koerdell, 1950], *Anacardites lanceolatus* Berry, *Anona saraviana* Berry, *Bignonoides orbicularis* Berry, *Connarus carmenensis* Berry, *Crescentia cucurbitinoides* Berry, *Dioclea? mexicana* Berry, *Drypetes elliptica* Berry, *Fagara wadii* Berry, *Ficus? talamancana* Berry, *Goeppertia* cf. *G. tertiaria* Berry, *Gouania miocenica* Berry, *Guettarda cookei*? Berry, *Lecythidophyllum couratarioides* Berry, *Leguminosites oaxacensis* Berry, *Melastomites angustus* Berry, *M. obovatus* Berry, *Moquillea mexicana* Berry, *Myrcia saraviana* Berry, *Nectandra areolata* Engelhardt, *N. tehuantepecensis* Berry, and *Rondeletia*? sp.

The second locality is in the state of Veracruz near San José del Carmen, southeast of Coatzacoalcos. The village is an outlier of the larger adjacent settlement of Las Choapas about 25 km S of Mexico 180. The flora consists of *Gymnogramme wadii* Berry [*Gymnocladus wadii* (Berry) Maldonado-Koerdell, 1950], *Allamanda carmenensis* Berry, *Apocynophyllum mexicanum* Berry, *Cedrela miocenica* Berry, *Connarus carmenensis* Berry, *Coussapoa veracruziana* Berry, *Inga miocenica* Berry, *Leguminosites mexicanus* Berry, *Liquidambar incerta* Berry, *Melastomites obovatus* Berry, *Mespilodaphne palomarensis* Berry, and *Simaruba veracruziana* Berry.

Later, Mullerried (1938) described *Juglans veracruzana* from Tertiary deposits near Tlacolulan, just northwest of Jalapa, and Miranda (1963) recorded *Acacia* sp. and *Tapirira durhamii* Miranda from Oligo-Miocene ambers near Simojovel in the state of Chiapas. Breedlove (pers. comm., 1971) notes the presence of fragmentary plant remains in Chiapas, and in 1961 specimens of well-preserved angiosperm leaves were examined in the posada of Franz Blom, San Cristóbal. These had been collected by local inhabitants and the source was unknown. Considering the depositional environments along the eastern coastal plain of southern Mexico, it is likely that numerous fossil plant localities



Figures 86–113.—86–92, 94. Compositae.—86–87. Type 1, 19-1, T-30,1-3, 63 μ.—88. Type 2, 17-1, W-10, 34 μ.—89. Type 3, 10-1, V-41, 45 μ.—90. Type 4, 17-1, P-11,3, 37 μ.—91, 94. Type 5, 25-1, X-38,4, 21 μ.—92. Type 6, 2-1, U-38,1, 27 μ.—93, 95–97. *Lagunclaria*.—93. 25-1, V-25,2, 22 × 15 μ.—95. 33-1, K-32, 23 × 16 μ.—96. 25-1, J-20,3, 27 × 22 μ.—97. 30-1, W-31,3-4, 29 × 22 μ.—98–102. *Combretum/Terminalia*—98. 17-1, Q-47, 1-3, 32 × 20 μ.—99. 17-1, N-16,1, 32 × 20 μ.—100. 17-1, X-32,2-4, 27 × 19 μ.—101. 17-1, W-17,3-4, 29 × 18 μ.—102. 17-1, W-9,3, 29 × 20 μ.—103–106. *Rajania*.—103,106. 4-1, 0-34,3-4, 30 × 22 μ.—104. 2-1, W-42,3, 34 × 25 μ.—105. 2-1, W-18, 35 × 24 μ.—107–113.

occur scattered through Veracruz, Oaxaca, and Chiapas. Because of the inaccessibility of much of the country and the brief exposure of new sites from the surrounding vegetation, detailed and sustained studies of Tertiary megafossil floras will most efficiently be made by resident investigators.

None of the above floras have been revised since original publication. From the collective list only *Acacia*, *Cedrela*, *Juglans*, and *Liquidambar* are represented as pollen in the Paraje Solo microflora.

Paleoenvironments

The physical environment of southeastern Veracruz has been relatively stable during middle and late Cenozoic times. Relative sea level was slightly higher as evidenced by mangrove-containing lignites of the Paraje Solo Formation 8–12 m above present shorelines. The principal volcanic activity was uplift of the Sierra de Los Tuxtlas (1,700 m) beginning in the Miocene and culminating in the Plio-Pleistocene. Although these events modified local landscapes, major features of the physical environment were defined at the end of the Cretaceous and during the early Tertiary.

In the preceding discussion of Miocene communities certain differences were noted between the modern and ancient plant associations of southern Veracruz. These were: presence of a few genera now absent from Veracruz (notably *Picea*; Table 4), the expanded range of certain communities (Deciduous Forest), absence or poor representation of the Tropical Rain Forest, absence or poor representation of communities characteristic of dry to arid habitats, and absence or poor representation of vegetation types suspected, but not proven, to have originated, persisted and/or expanded under anthropogenic influence.

Several of these features of the paleocommunities can be attributed to slightly lower temperatures and possibly greater or more uniform distribution of rainfall during the upper Miocene than at present. The presence of well-preserved unfragmented pollen of *Picea*, a genus currently found only at high elevations (2,300–3,200 m; Gordon, 1968) over 1,000 km to the north (Chihuahua, Durango, Nuevo León), suggests cooler climates. A lowering of temperatures and increased or more uniformly distributed rainfall, however, in a floristically and topographically diverse region as Veracruz would have significant effect on several communities and these effects should be reflected in the composition of the fossil pollen flora.

One community particularly susceptible to lower temperatures would be the lowland Tropical Rain Forest, and this vegetation type is poorly represented in the Paraje Solo sediments. A comparison in Fig. 5 of the High Evergreen Selva (25 genera listed) with the oak-*Liquidambar* forest (29 genera) initially suggests comparable representation. However, for the oak-*Liquidambar* forest

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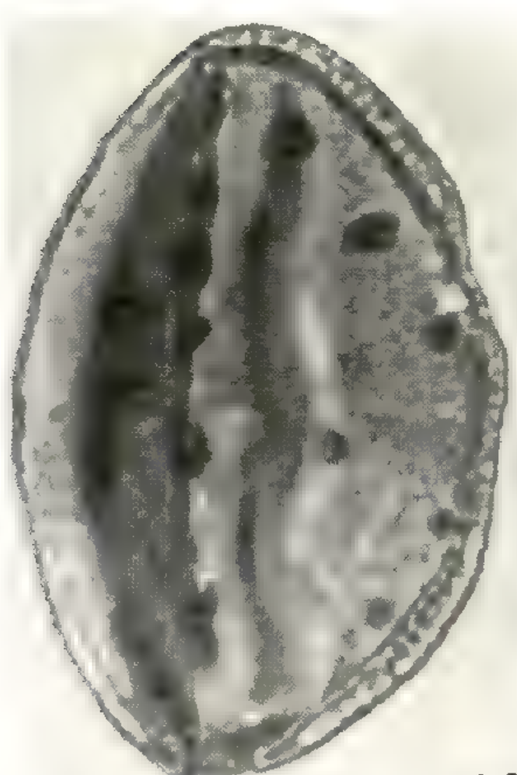
Quercus.—107. 17-1, U-43,2-4, 35 × 24 μ.—108. 13-1, R-32,4, 41 × 31 μ.—109. 13-1, S-14,1, 37 μ.—110–111. 6-1, T-19,3-4, 32 × 24 μ.—112. 17-1, X-36,3, 32 × 26 μ.—113. 13-1, M-12,2, 35 × 27 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]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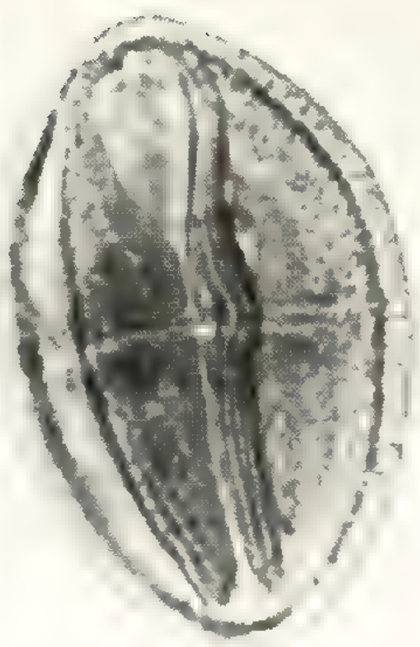
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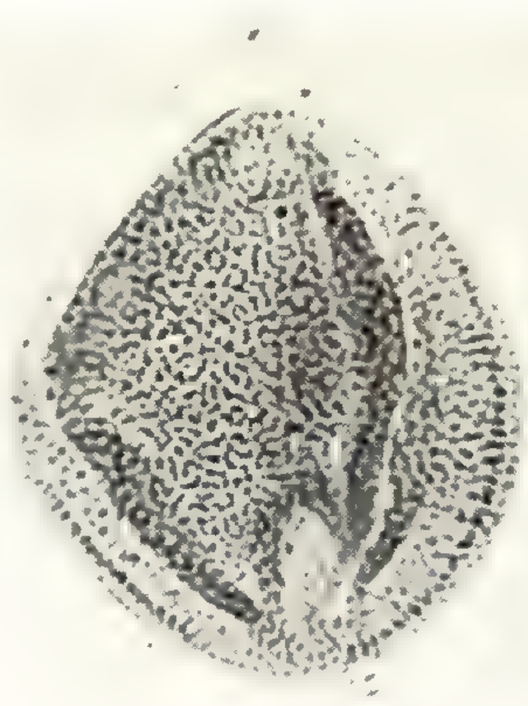
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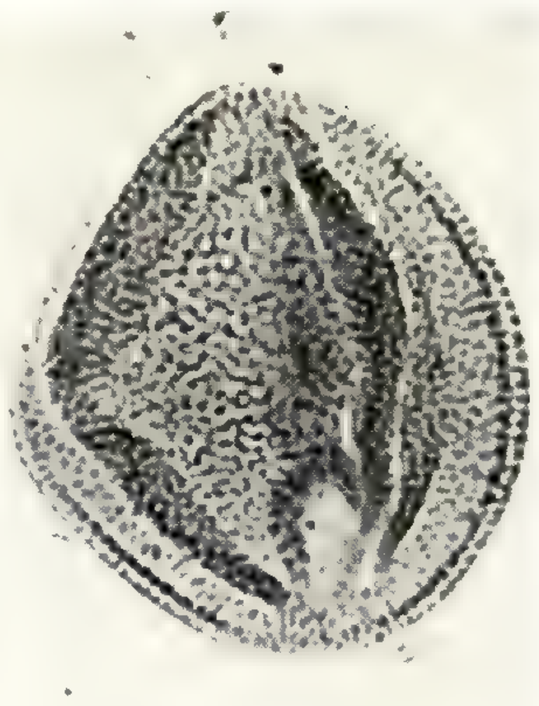
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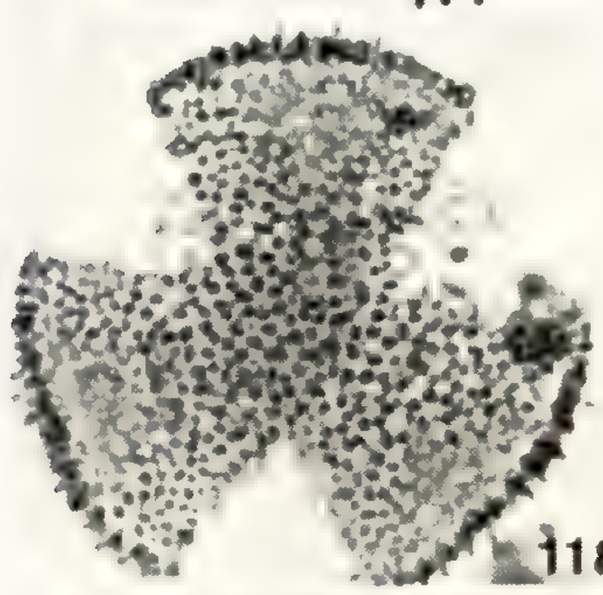
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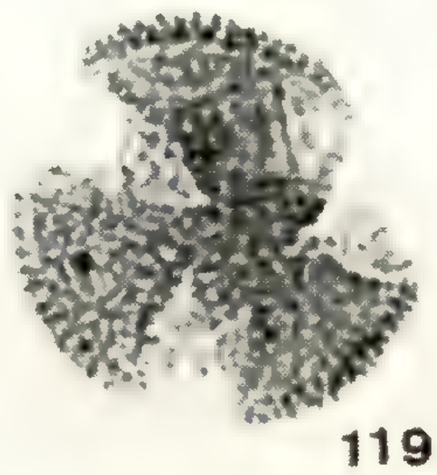
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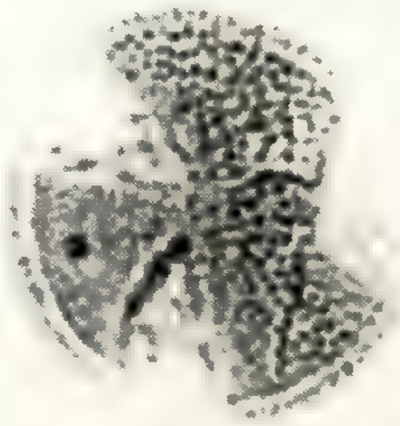
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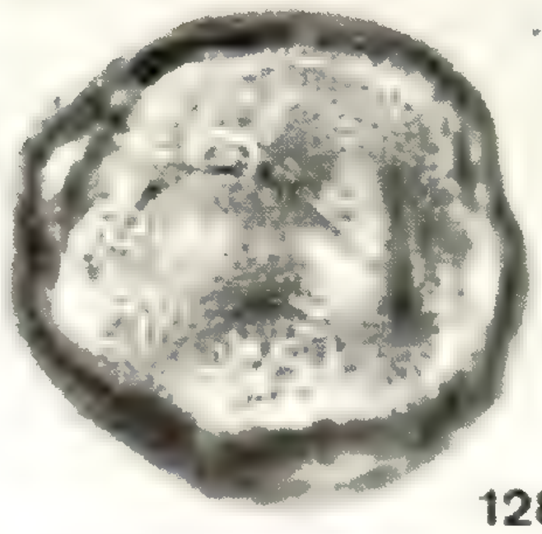
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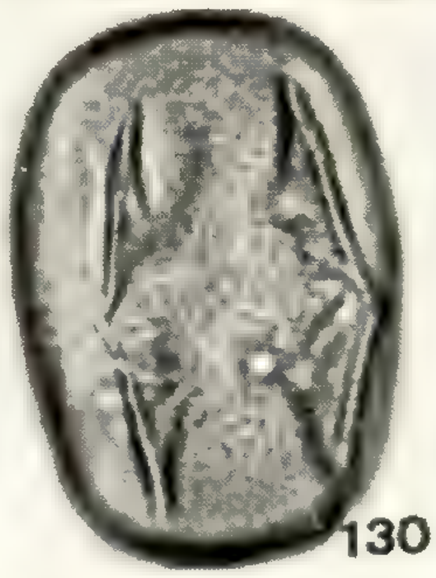
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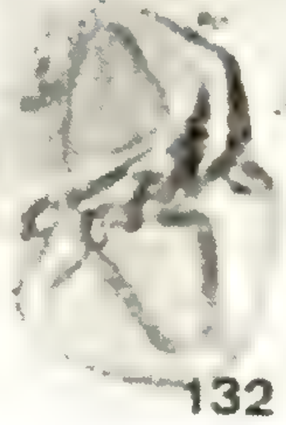
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FIGURES 114–136.—114. Cf. *Stillingia*, 8-1, R-23, 54 × 36 μ.—115. Cf. *Sapium*, 9-1, S-39,3, 58 × 41 μ.—116–117. *Tithymalus*, 15-1, G-15,3-4, 50 × 45 μ.—118–120. Cf. *Tetrorchidium*.—118. 54-1, T-44,1, 52 μ.—119–120. 34-1, F-21,3, 36 μ.—121. *Liquidambar*. 2-1, H-30,3-4, 38 μ.—122–123. Cf. *Bernardia*, 10-1, B-13,3, 41 × 28 μ.—124–125. *Casearia*, 6-1, V-18,3, 27 × 22 μ.—126. *Juglans*, 54-1, Y-38,2-4, 36 μ.—127–128. *Laetia*, 8-1, H-27, 49 μ.—129–130. *Gustavia*, 25-1, 0-40, 52 × 35 μ.—131–132. *Mimosa*.—131. 19-1, E-21,3-4, 27 μ.—132. 19-1, U-14,4, 36 × 25 μ.—133–136. *Engelhardtia*.—133. 2-1, U-28,1, 32 μ.—134. 13-1, Q-37,2, 23 μ.—135. 2-1, W-32, 27 μ.—136. 2-1, U-35,3, 23 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

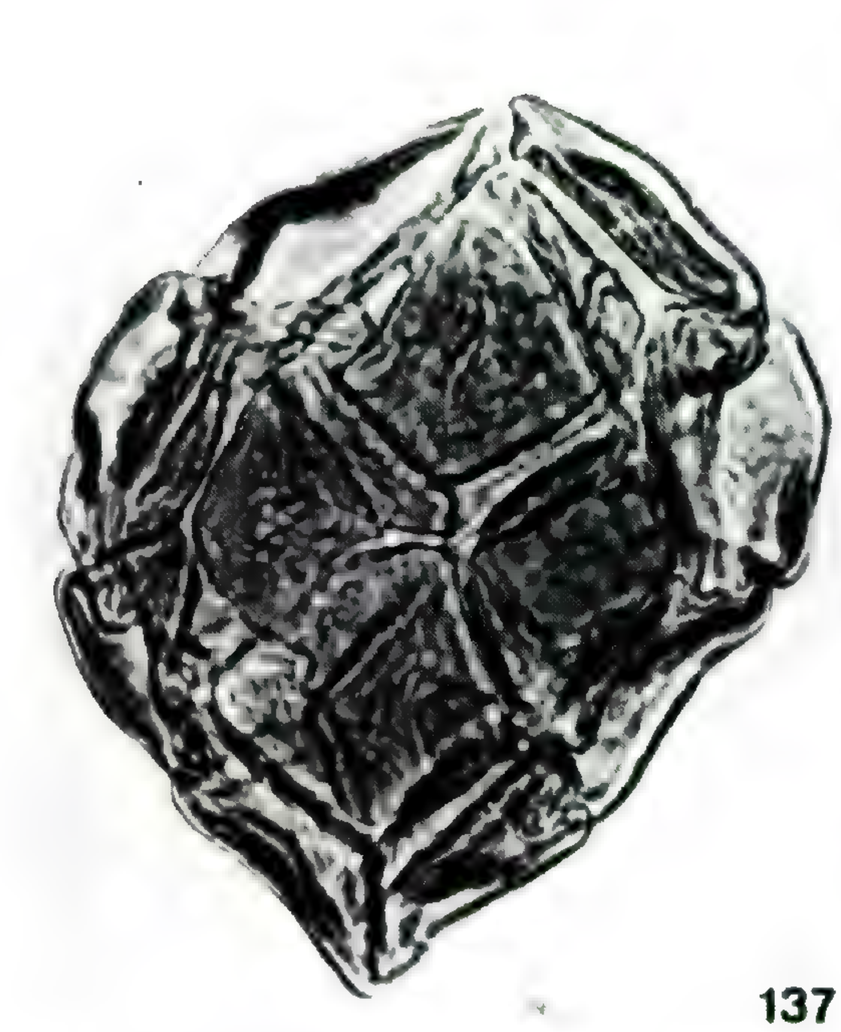
both dominants and a number of characteristically associated genera are present. Among the genera listed for the High Evergreen Selva, none of the dominants of the modern rain forest in Veracruz were recovered with the possible exception of *Terminalia amazonia* (J. F. Gmelin) Exell (identified as *Combretum/Terminalia*). Of the 25 genera present, 17 occur in other types of vegetation, one (*Allophylus*) occurs in secondary (disturbed) vegetation, one is a tentative identification (cf. *Hiraea*), and two have pollen similar to other nonrain forest genera (*Combretum/Terminalia, Eugenia/Myrcia*). Comparable results are being obtained by Palacios Chavez (unpublished data) for Tertiary deposits in Chiapas. In these sediments pollen of *Picea* was present and pollen of rain forest genera scarce or absent.

Regarding the absence of the dominant defining elements of the modern Veracruz rain forest in the Paraje Solo microflora, it is unlikely that this can be attributed entirely to low pollen production associated with entomophily. Although pollen of *Ficus tecolutensis* (Liebm.) Miq. would not be expected, the insect pollination of others is not so strict as to preclude entry of pollen into the sedimentary record (i.e., *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoullia flammea* Oliver, *Brosimum alicastrum* Swartz, *Pseudolmedia oxyphyllaria* Donnell Smith; Rzedowski, pers. comm., 1974; Baker, pers. comm., 1975). Further, it is a characteristic of Tertiary microfloras from tropical regions that they contain pollen of entomophilous species (e.g., *Hibiscus*-type, Figs. 154, 156). This is probably due to "outwashing" of pollen under high rainfall regimes, particularly from lowland communities bordering basins of deposition (Germeraad et al., 1968: 206).

Within the complex mosaic of vegetation occupying the lowlands and adjacent slopes in Veracruz, there are diverse ecotypes capable of aggregating into various kinds of communities depending on the existing set of environmental conditions. Sarukhán (pers. comm., 1974) has suggested that if the Tropical Rain Forest were disrupted by slightly lower temperatures, expansion of the warm oak community of *Quercus oleoides* Cham. & Schlecht. would likely be favored. This suggestion is of interest because in these sediments where evidence for Tropical Rain Forest is meager, pollen of *Quercus* reaches 34% at site 6 (Table 1), far greater than would be expected from upland oak communities (Bosque de Pino y Encino; temperate and evergreen oak forests).

Gómez-Pompa (1973: 110), discussing a species list from the High Evergreen Selva, comments that: "Three species on this list that need further discussion are *Podocarpus guatemalensis*, *Quercus oleoides*, and *Sphaeropteris myosuroides*. They seem to be out of place in this type because, with the exception of *Sphaeropteris*, they have not been found growing in these selvas in any other areas in Veracruz, or even in Mexico. I cannot find any environmental explanation for this coincidence. The only possible explanation is that they are relicts of the old community that seems to have grown in these areas in the recent geological past when the area was cooler." The genus *Myrica* has also been found recently in the Veracruz lowlands, disjunct from its more common occurrence in the temperate upland Deciduous Forest.

Another relevant aspect of the microflora is the apparent lowering of eco-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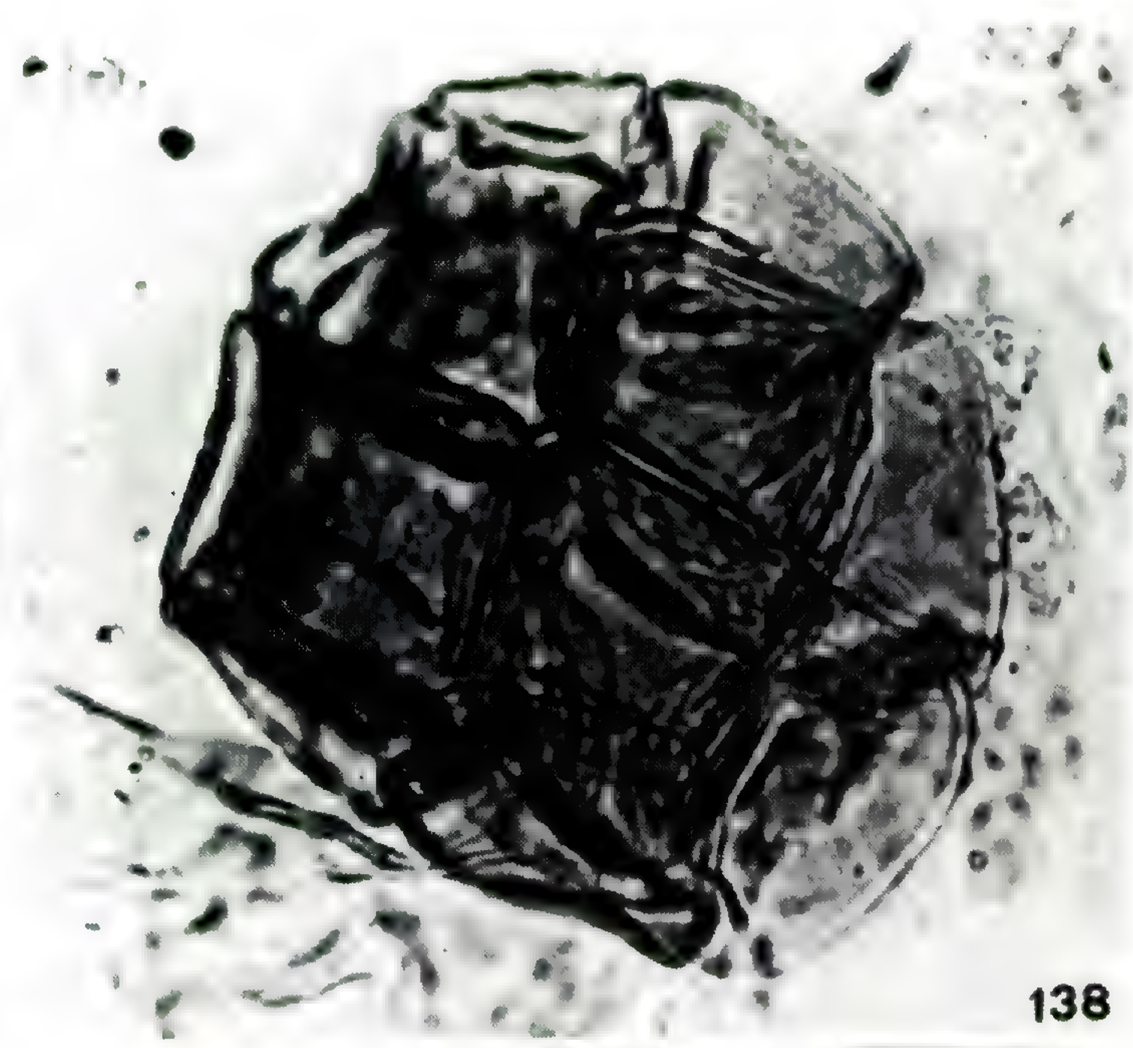
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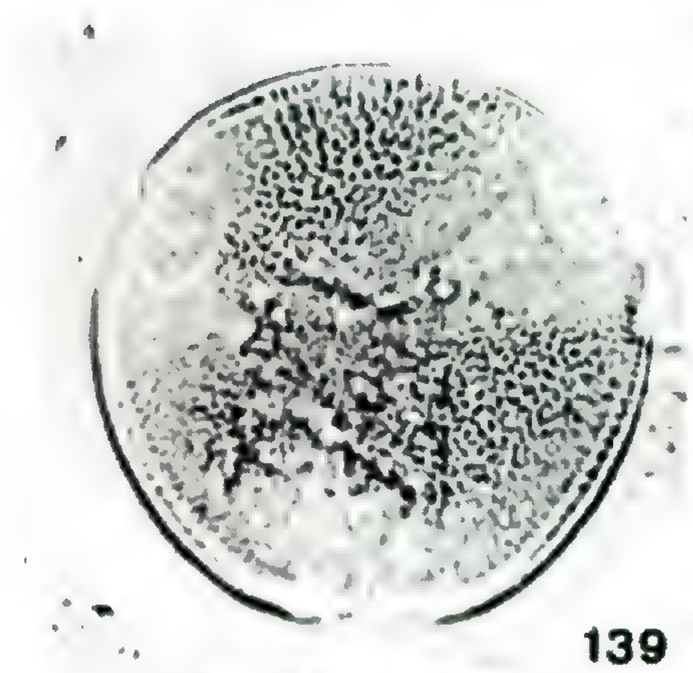
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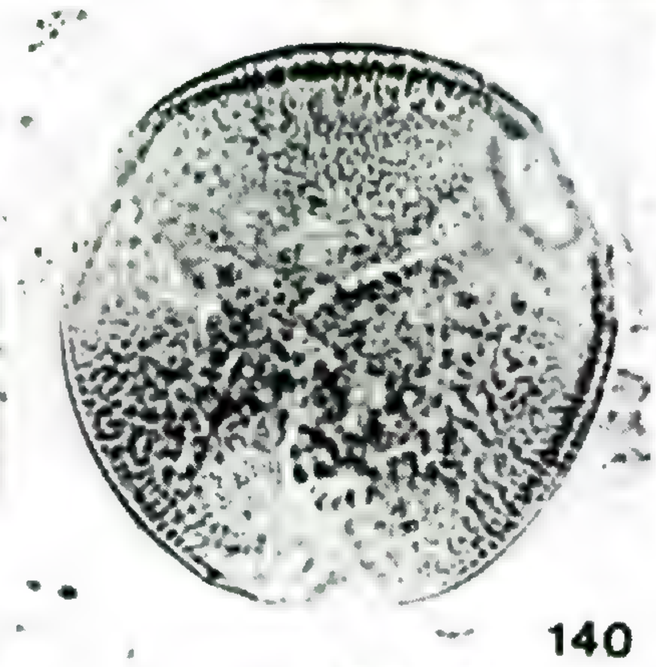
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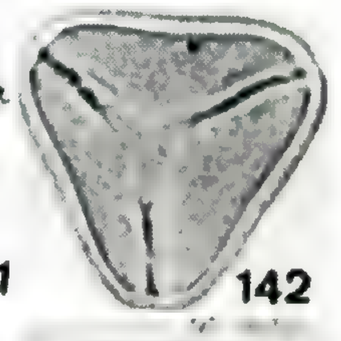
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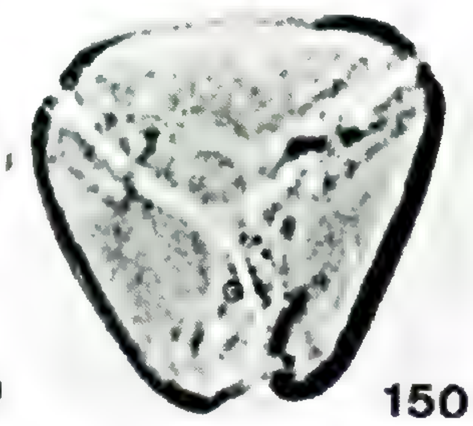
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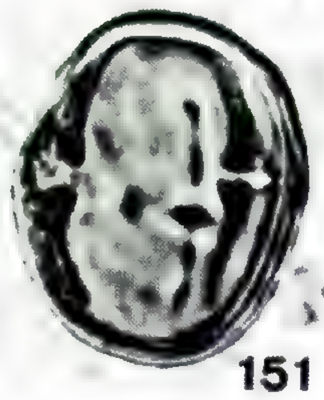
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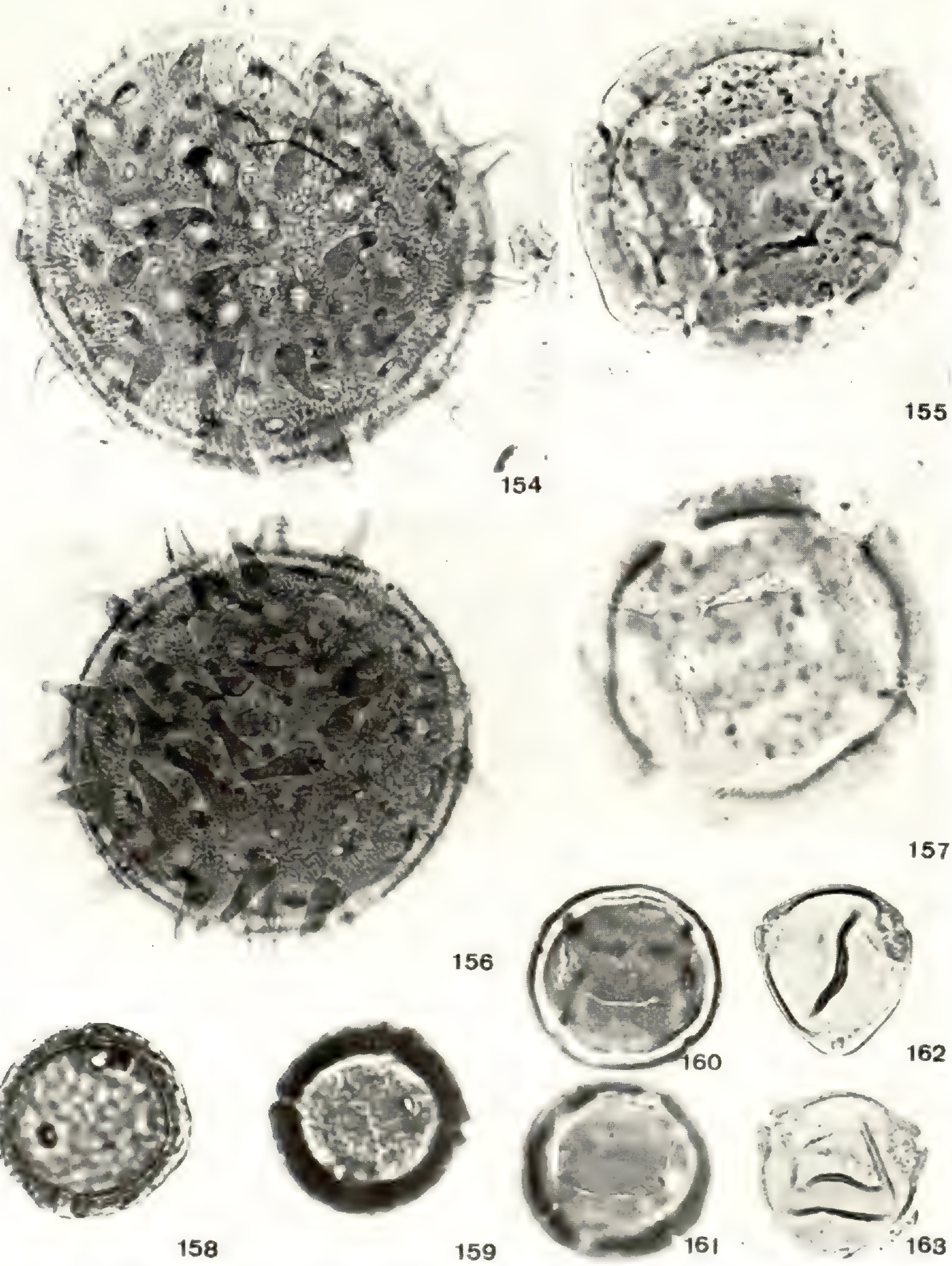
Figures 137–153.—137–138. Cf. *Acacia*.—137. 13-1, Q-15,4, 87 × 72 μ.—138. 44-1, T-37,1-3, 85 μ.—139–140. *Desmanthus*, 15-1, W-21,2-4, 58 μ.—141. *Cuphea*, 25-1, V-49,4, 31 μ.—142–144, 147–150. *Struthanthus*.—142. 49-1, K-26,2, 36 μ.—143. 38-1, K-32,2, 24 μ.—144. 32-1, X-42, 31 μ.—147. 4-1, E-41,2, 30 μ.—148. 4-1, R-40,1, 32 μ.—149. 17-1, E-18,3, 30 μ.—150. 4-1, C-28,4, 36 μ.—145–146. *Utricularia*.—145. 19-1, J-46,3, 54 μ.—146. 33-1, L-30,2, 49 μ.—151. *Cedrela*, 10-1, S-9, 40 × 31 μ.—152–153. *Guarea*.—152. 13-1, S-25,1, 30 μ.—153. 6-1, W-19,1-3, 32 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

tones, bringing the Needle-Leaved Forest (*Abies*) and especially the Deciduous Forest into closer proximity to the depositional basin. The presence of these communities, well represented in the microflora, can most easily be explained by an extension of the Deciduous Forest ecotone below its present limit of about 1,000 m.

The introduction of temperate trees and shrubs disjunct from the deciduous forest of the eastern United States has been considered earlier (Graham, 1972, 1973). The opportunity for migration of some of these elements from north to south is based on late Tertiary climatic trends toward cooler conditions, and their early record in Eocene deposits of the Mississippi Embayment (Gray, 1960) with progressively later occurrences of a diminishing number of genera to the south. Approximately 60 species of arborescent plants are common to the temperate forests of the eastern United States and eastern Mexico (Graham, 1973: table 1). Estimates of the principal time of introduction of these plants into Mexico (Cretaceous to Pleistocene) includes virtually the entire geologic range of the angiosperms, primarily because adequate paleobotanical data was not available for eastern Mexico. The most commonly cited time of introduction is the Pleistocene (Deevey, 1949), when presumably elements of the eastern deciduous forest were forced into southern refugia during times of maximum glaciation. Although this is possible, data from the Paraje Solo assemblage in Veracruz document that some elements were already established in southeastern Mexico by late Miocene times. The earliest time of introduction is not known, but pollen of these temperate plants was not recovered from the Oligo-Miocene Simojovel Group of Chiapas (Langenheim et al., 1967). The late Miocene is an appropriate time for the range of some elements of the deciduous forest to expand into southern Mexico since world climatic models document that the climatic cooling, ultimately culminating in the Pleistocene glaciations, was already evident by the end of the Miocene (see summaries in Flint, 1971; Garner, 1974). Considering the number of taxa involved, however, (ca. 60 species of trees and shrubs plus herbaceous plants) it is probably that factors other than progressive introduction are involved in the complex relationships that exist between the eastern United States and eastern Mexico.

Axelrod (1975) has suggested a further explanation for these "Appalachian" disjuncts in the Mexican cloud forest. Rather than migrants from the north, he considers the modern vegetation along mid-altitude portions of the eastern Mexican Plateau as remnants of a "temperate rainforest" that during the early Tertiary (Eocene) extended in modified form into the Appalachian and other regions of the United States. As a result of later Cenozoic cooling climates, the evergreen portion of this community diminished in the north, leaving a predominantly temperate deciduous forest while the mixed temperate/evergreen community persisted in eastern Mexico.

Ultimately, the model that adequately reflects the origin of floristic and faunal relationships between the eastern United States and eastern Mexico will probably provide a number of means whereby various elements of the complex could become established. As noted earlier, progressive introduction from the north is only one of several pathways available, and probably utilized by a



FIGURES 154–163.—154, 156. *Hampea*/*Hibiscus*.—154. 44-1, 0-23, 135 μ.—156. 45-1, U-42, 1-2, 144 μ.—155, 157. Cf. *Mezia* (?) type, 19-1, F-15,4, 74 μ.—158–159. Cf. *Malpighia*, 5-1, P-27, 36 μ.—160–161. Cf. *Hiraea*, 2-1, L-23,2, 47 μ.—162–163. *Myrica*.—162. 10-1, J-44, 36 μ.—163. 15-1, M-15, 33 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

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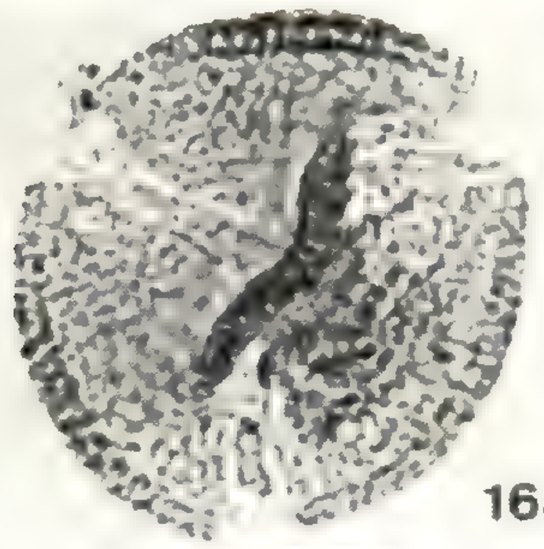
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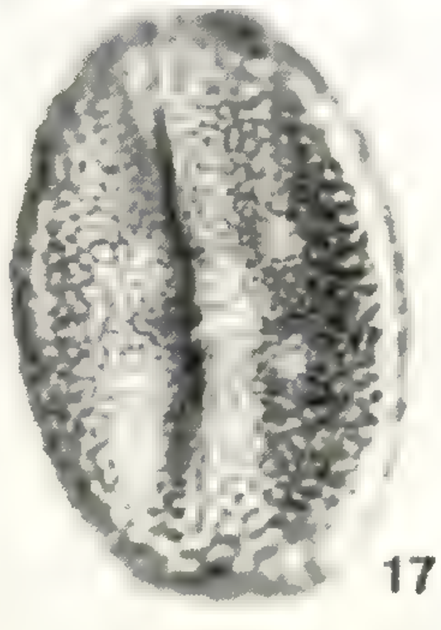
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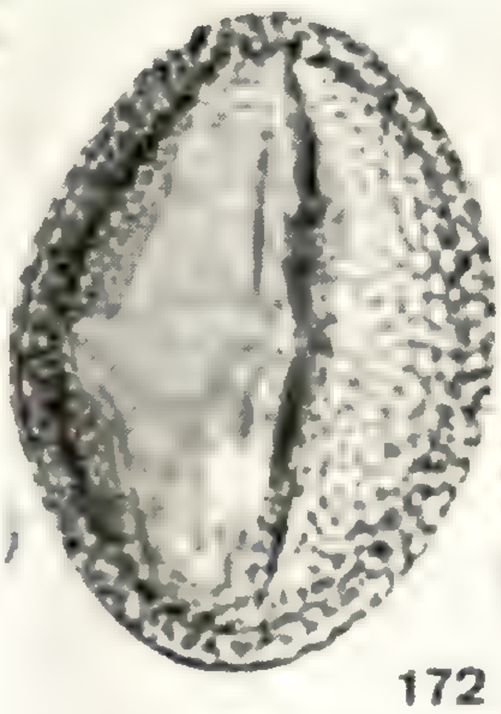
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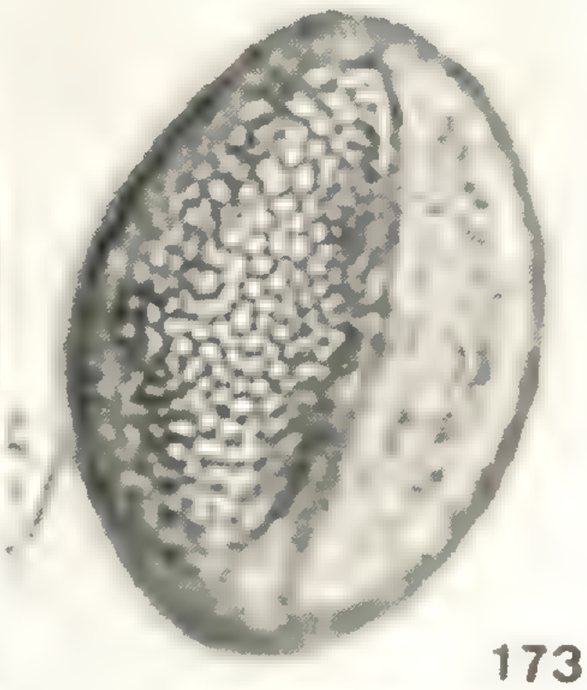
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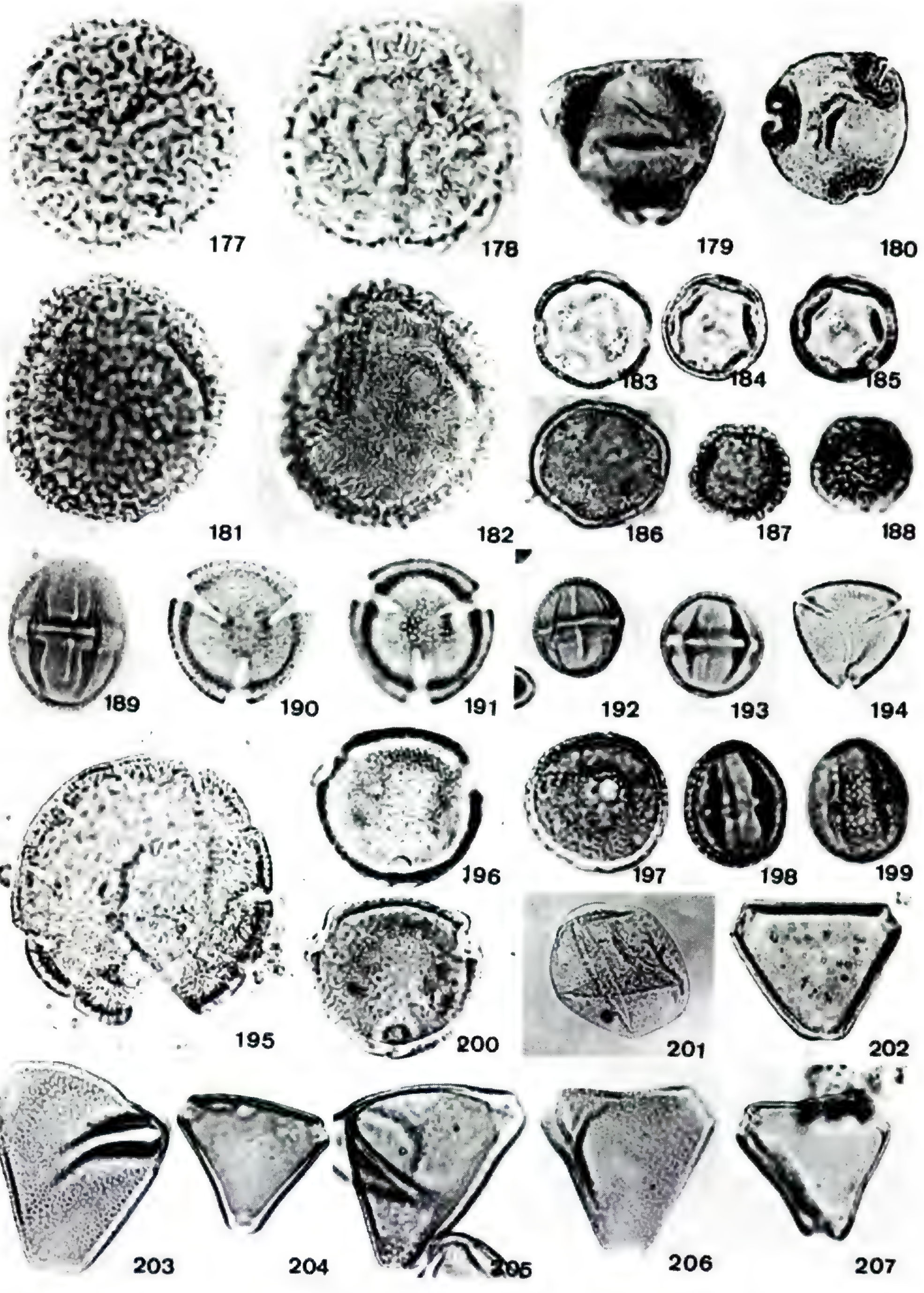
FIGURES 164–176.—164, 169, 174. *Ludwigia* (*Jussiaea*).—164. 30-1, J-40,2-4, 104 μ.—169. 15-1, E-36,1, 90 μ.—174. 33-1, G-28,1-3, 72 μ.—165. Cf. *Securidaca*, 13-1, L-10,1, 36 μ.—166–167. Cf. *Bredemeyera*, 13-1, E-21,3-4, 31 $\times$ 27 μ.—168, 170–173, 175–176. *Coccoloba*.—168. 17-1, Q-42,2, 42 μ.—170–171. 30-1, K-40, 54 $\times$ 33 μ.—172–173. 30-1, P-26,3, 58 $\times$ 40 μ.—175–176. 32-1, X-31,2-4, 40 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]



Figures 177–207.—177–178, 181–182. *Passiflora.*—177–178. 19-1, X-24,4, 49 μ.—181–182. 2-1, P-38,1, 55 μ.—179–180. *Faramea.*—179. 9-1, P-33, 34 μ.—180. 13-1, G-17,1-2, 32 μ.—183–186. *Thalictrum.*—183. 13-1, Y-34,1, 26 μ.—184–185. 13-1, X-27,2-4, 24 μ.—186. 17-1, T-29,1-3, 27 μ.—187–188. *Terebrania,* 7-1, 0-20, 22 μ.—189–193. *Rhizophora.*—189. 10-1, X-46,4, 30 × 24 μ.—190–191. 4-1, L-18,1-2, 29 μ.—192. 51-1, R-35,2-4, 26 × 23. μ.—193. 10-1, V-43,4, 23 μ.—194. *Eugenia/Myrcia,* 13-1, Q-30,1, 23 μ.—195. *Borreria,* 15-1, U-22,1, 59 μ.—196–197, 200. *Alibertia.*—196, 200. 15-1, L-29,2, 32 μ.—197. 33-1,

limited number of organisms. Periodic introductions throughout the Cenozoic via long-distance dispersal, and Quaternary migrations as envisioned by Deevey (1949) are also possible. Axelrod's (1975) valuable summary provides a plausible explanation for the occurrence of others. The need for further information on pre-upper Miocene Tertiary floras from southeastern Mexico is clearly evident. The meager paleobotanical data, from a single relevant study (Langenheim et al., 1967; Oligo-Miocene of Chiapas) does not record the presence of eastern United States-eastern Mexican arborescent temperate elements in Chiapas at that time.

In summary, slightly lower temperatures and greater or more uniformly distributed rainfall appears to be a logical and convenient factor in explaining the principal differences between modern and Miocene plant communities of southeastern Veracruz: the presence of *Picea*, poor representation of the High Evergreen Selva, locally extensive warm oak forests, presence of occasional temperate species in the tropical lowlands, prominent representation in lowland sediments of high altitude Needle-Leaved and mid-altitude Deciduous Forest, and the appearance of Arcto-Tertiary elements in northern Latin America corresponding in time to early phases of world-wide climatic cooling. Other consequences of lower temperatures would be increased likelihood of Paramo vegetation at the highest elevations, as previously discussed, and expanded range of the temperate grassland now preserved as relicts [*Bouteloua curtipendula* (Michx.) Torr. and *B. gracilis* (H.B.K.) Lag. ex Steud.] in the Valley of Perote.

On the basis of results from the Veracruz study, it is interesting to speculate on the history and development of the Tropical Rain Forest in Veracruz. As noted earlier, the effect of cooling climate was already evident world-wide by the end of the Miocene, continued through the Pliocene, and eventually culminated in the Pleistocene glaciations. If the rain forest was poorly developed in southeastern Veracruz in the upper Miocene because of lower temperatures, there would have been little chance for expansion and permanency during the Pliocene and Pleistocene when climates were becoming even cooler. This raises the interesting possibility that, although elements were present throughout the middle and upper Cenozoic, the High Evergreen Selva near its northern limits in Veracruz did not develop into a defined and extensive community of modern aspect and composition until post-glacial times of about 18,000–11,000 years ago (for recent discussion on dates for the end of the glacial period as evidenced in the western Gulf of Mexico, see Kennett & Shackleton, 1975). This view is in contrast with most of the older biogeographic literature which depicts the Tropical Rain Forest as an ancient assemblage occupying regions of stable, unchanging environments, and is consistent with more recent data suggesting con-

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E-34,4, 28 μ.—198–199. *Meliosma*, 40-1, U-34,3, 27 × 23 μ.—201. *Populus*, 2-1, B-27, 36 μ. —202–203. *Paullinia*.—202. 8-1,V-49,3-4, 35 μ.—203. 10-1, G-26,4, 36 μ.—204–207. *Serjania*. 204. 25-1, L-38,2-4, 27 μ.—205. 4-1, U-16,1, 36 μ.—206. 49-1, Q-43,1, 40 μ.—207. 13-1, J-25,2, 35 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

Figures 208–226.—208. *Allophylus*, 10-1, N-24,3, 25 μ.—209. *Cupania*, 2-1, G-22,1, 28 μ.—210–211. *Matayba*.—210. 2-1, N-44,3, 31 μ.—211. 25-1, N-12, 22 μ.—212–214. *Buettneria*.—212. 13-1, W-43, 23 μ.—213–214. 37-1, F-25, 27 μ.—215–218. *Cleyera*.—215. 17-1, T-11, 32 × 24 μ.—216. 33-1, J-48,2, 27 μ.—217–218. 17-1, U-25, 28 × 24 μ.—219–221. *Daphnopsis*.—219. 17-1, P-11, 36 μ.—220. 25-1, T-39,3, 42 μ.—221. 17-1, H-12,2, 40 μ.—222–223. *Celtis*.—222. 17-1, U-45, 32 μ.—223. 2-1, C-50,1, 35 μ.—224–226. *Ulmus*.—224. 38-1, M-33,3, 36 μ.—225. 33-1, N-48,1-2, 31 μ.—226. 37-1, M-13,1, 34 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

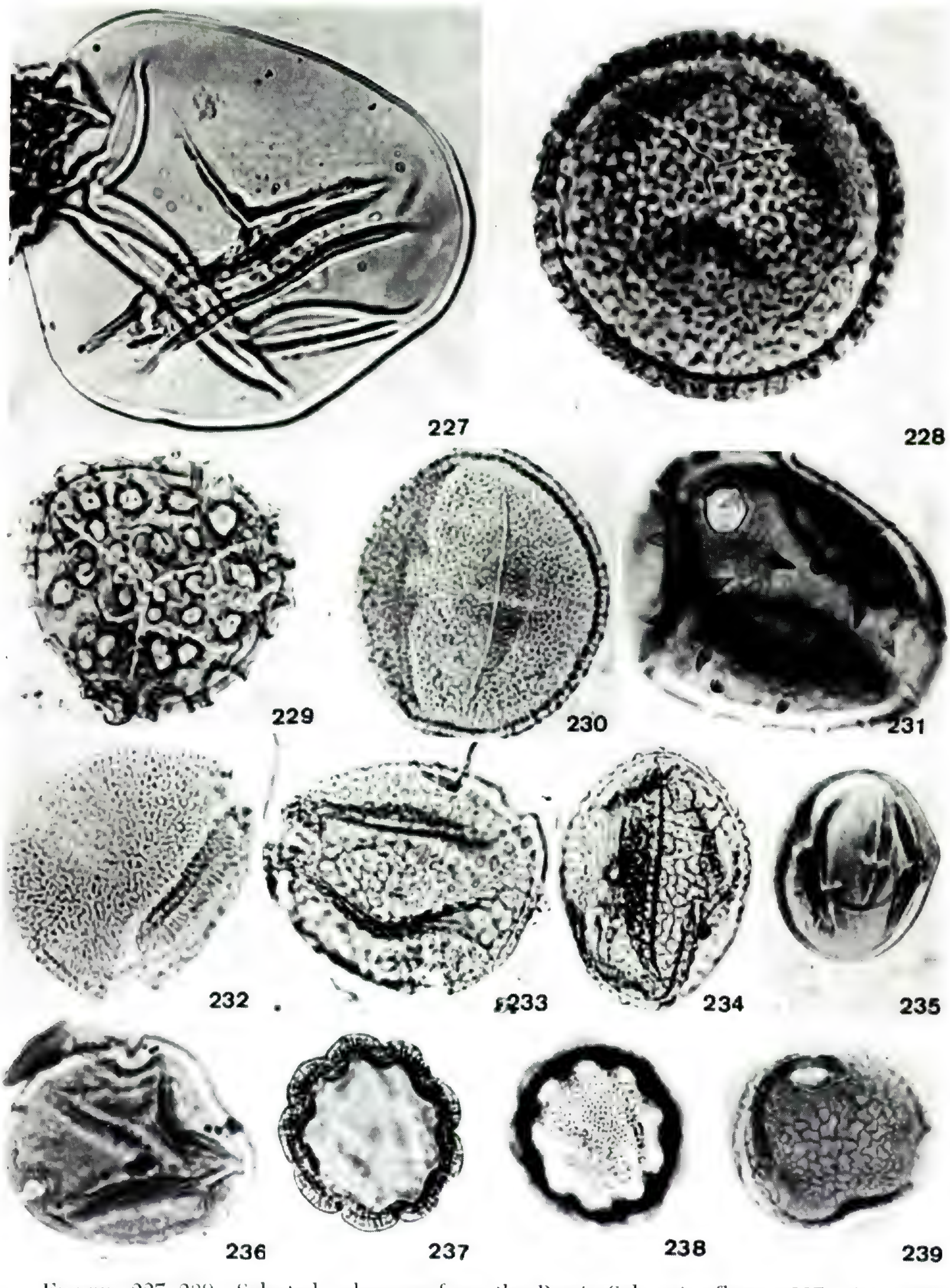
siderable alteration in range and composition of the rain forest during the last few million years (Haffer, 1969, 1970, 1974; Vanzolini, 1973; Vanzolini & Williams, 1970; Vuilleumier, 1971). The relevancy of this new concept of rain forest history to speciation models is briefly discussed by Graham (1975).

Regarding moisture regimes during the upper Miocene, there is some evidence for slightly increased rainfall or more uniform distribution with no pronounced dry season. Sousa (pers. comm., 1973) believes fossil pollen of *Picea* in Veracruz implies more moisture as well as cooler climates. This view is supported by the absence of desert vegetation and only minor representation of the Low Evergreen Selva, Low Thorn Selva, and Thorn Scrub. The presence of *Cupania*, *Celtis*, *Casearia*, *Daphnopsis*, *Eugenia*, *Ilex*, cf. *Acacia*, *Bursera*, cf. *Sapium*, *Comocladia*, cf. *Brahea*, and *Combretum* (Fig. 5) may reflect a modified Low Deciduous Selva occupying restricted areas of edaphically or physiographically induced moisture stress. These ecotypes are important in the dynamics of vegetational history since in more recent times they have coalesced with other pre-adapted subhumid elements to form the modern xeric communities of Veracruz. In the upper Miocene, however, they were not, as a community, a conspicuous or widespread component of the vegetation.

The last category of communities apparently absent from the upper Miocene landscape are those suspected of resulting from human activity. The natural origin and antiquity of the Low Semi-Evergreen Selva, Savannas, and Palm Stands (especially *Scheelea* and *Sabal*) in Veracruz have never been satisfactorily resolved. The prevalent view is that the present extent, if not the origin, of these associations resulted from agricultural practices of sedentary populations (milpa farming). These studies are relevant only in demonstrating that the Low Semi-Evergreen Selva, Savannas, and Palm Stands were not prominent members of the natural vegetation, and are at least of post-Miocene development.

The evolution of plant communities in southeastern Veracruz since the upper Miocene has involved three principal changes in the flora. Elements of the High Evergreen Selva have coalesced into the dominant natural community of the modern southern Veracruz lowlands, with concomitant elimination of *Picea* from Veracruz and elsewhere in southern Mexico (Ohngemach, unpublished data). This is likely due to increasing minimum temperatures, in contrast to those of the upper Miocene, and perhaps occurred as late as 18,000–11,000 B. P. (Kennett & Shackleton, 1975). Elements preadapted to arid environments expanded and coalesced into communities as a result of a slight decrease or redistribution of rainfall, but facilitated by the rise of the Sierra de Los Tuxtlas and more recently by human modification of the environment. The last stage in the evolution of the Veracruz flora has been the appearance of Low Semi-Evergreen Selvas, Savannas, and Palm Stands resulting more directly from human activity.

A complete statement on the Cenozoic history of vegetation in southeastern Veracruz will require further paleobotanical studies of progressively younger floras. Of particular importance will be pollen analytical studies of Pleistocene sediments. Two events during that epoch may prove to be critical in understanding certain features of the Veracruz flora. The Hypsithermal Interval (xerothermic period, pine maximum) is a debated aspect of Quaternary paleo-



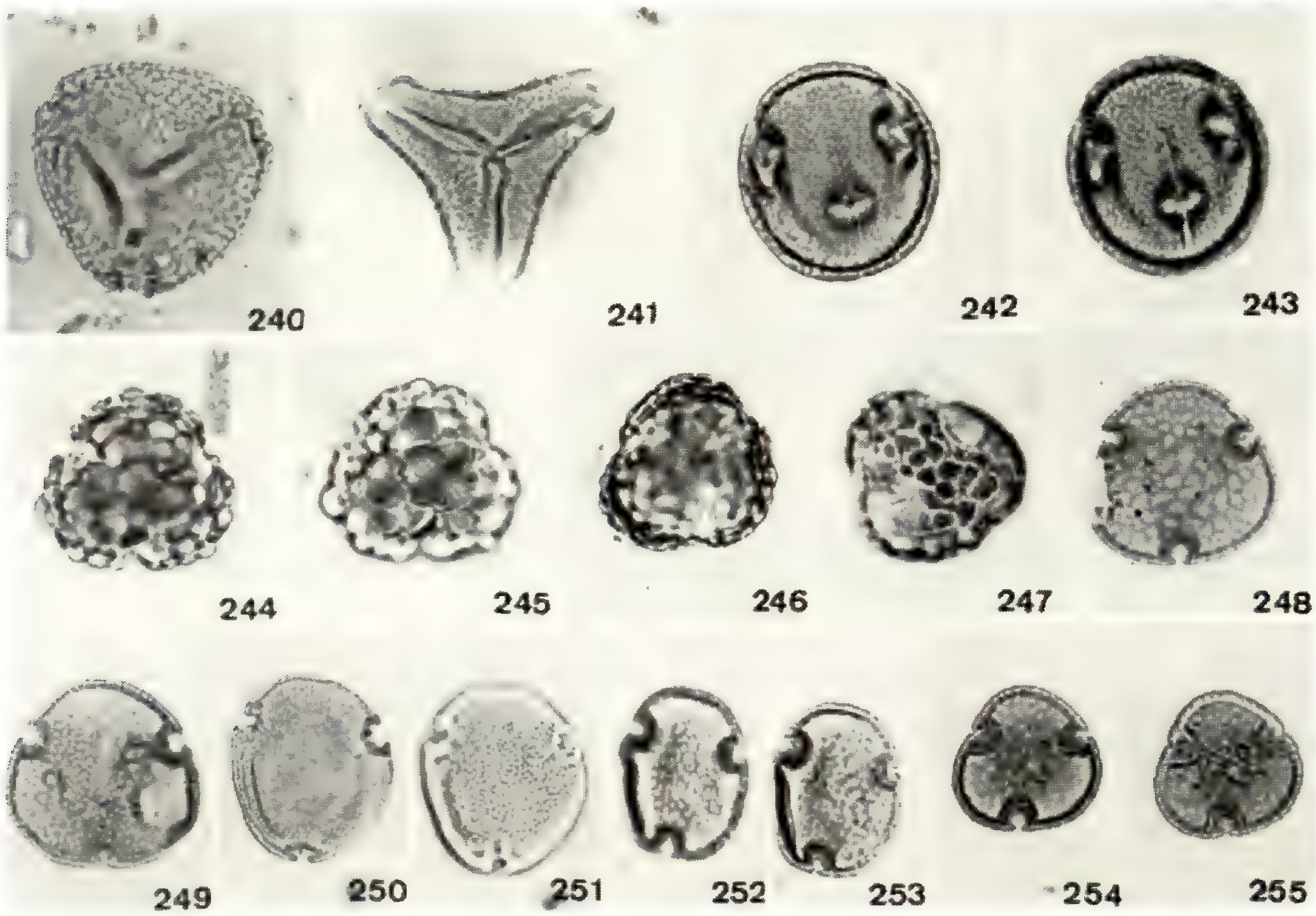
FIGURES 227–239. Selected unknowns from the Paraje Solo microflora.—227. 4-1, A-35, 2-4, 90 μ.—228. 30-1, B-23,1, 80 μ.—229. 10-1, C-45, 65 μ.—230–231. Cf. Cucurbitaceae.—230. 37-1, B-30,1-2, 65 × 55 μ.—231. 10-1, C-32,3, 75 μ.—232. Cf. Apocynaceae, e.g., *Thevetia*. 49-1, R-44,3, 55 μ.—233–234. Cf. *Mucuna*?.—233. 15-1, T-37, 58 μ.—234. 13-1, C-37,4. 60 × 45 μ.—235. Cf. Flacourtiaceae, e.g., *Zuelania*. 38-1, C-37, 40 × 35 μ.—236. 4-1, S-22,1, 45 μ.—237–238. Cf. Rubiaceae, 13-1, G-24, 44 μ.—239. 4-1, K-49, 49 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

ecology, especially in tropical regions. Broadly defined it is a period of about 4,000 years duration, between 8,000 to 4,000 B. P., during which climates were warmer and drier than at present. The closing date for the interval is of interest because Coe (pers. comm., 1973) and his associates have found evidence of a sedentary population in southern Veracruz dating from about 2,900 B. C. (ca. 4,900 B. P.). The Veracruz lowlands and adjacent regions are classically referred to as the "Olmec Heartland" and contains some of the earliest evidence of sedentary habitation in northern Latin America. Studies by Coe at San Lorenzo have shown that "pottery-using, sedentary, corn-growing peoples were in the area by 1,500 B. C. Three centuries later (ca. 1,200 B. C.) the archeological Olmec culture appears fully developed at San Lorenzo" (Coe, pers. comm., 1973). The earlier date of 2,900 B. C. is from a preceramic culture named by Jeffrey Wilkerson as Palo Hueco, at a site called Santa Luisa in the Tecolutea drainage. It is interesting to speculate on the consequences of an expanding farming population developing near the culmination of a climatically dry period. One effect may have been to accelerate the development and expand the range of Savannas, the Low Semi-Evergreen Selva, and Palm Stands. Evidence of a post-glacial dry period, anthropogenic modification of natural vegetation, and time of appearance of arid communities of plants would be significant contributions resulting from Quaternary pollen studies in southern Veracruz.

Conclusions

The upper Miocene paleocommunities of south coastal Veracruz show similarities and some distinct differences from present-day plant associations. Among communities well represented in the Paraje Solo assemblage are the Needle-Leaved Forests of Bosque de Oyamel (including *Picea* now restricted to the highlands of northern Mexico), Bosque de Pino, and Bosque de Pino y Encino; a lowland warm oak, and possibly upland temperate and evergreen Broad-Leaved Forest; Bosque Caducifolio (oak-*Liquidambar* Deciduous Forest); Saline and possibly Temperate Grasslands; Mangrove Swamps; Coastal Dune Vegetation; and vegetation occupying restricted areas of physiographically or edaphically controlled moisture deficits comparable to a modified Low Deciduous Selva. Other communities likely present were the Paramo, Inland Swamps, and Aquatic Vegetation, even though for reasons discussed, pollen of the dominants are absent or poorly represented in the microflora.

Other vegetation types forming an important part of the modern flora were not major components of the upper Miocene vegetation. These include the High Evergreen Selva, High Semi-Evergreen Selva, Medium Semi-Evergreen Selva, Low Evergreen Selva, Low Semi-Evergreen Selva, and communities of more arid aspect as the Scale-Leaved Forest, Low Thorn Selva, *Nolina-Hechtia-Agave* Desert, and Thorn Scrub. Two communities possibly resulting from ancient agricultural practices in the "Olmec Heartland" (Palm Stands and Savannas) were also poorly represented in the microflora. A change in two environmental factors simultaneously explains both the wide-spread occurrence of temperate communities and the restricted distribution of tropical and arid vegetation. It is



Figures 240–255. Selected unknowns from the Paraje Solo microflora.—240. 32-1, W-16,3, 36 μ.—241. Loranthaceae, 2-1, D-12,1-3, 42 μ.—242–243. Cf. Flacourtiaceae, e.g., *Laetia*, 35-1, R-18,2, 32 μ.—244–245. Cf. *Calamus*, Palmae, Old World; cf. one grain of a polyad of *Dichrostachys*, Leguminosae, Old World, 2-1, C-40,2-4, 40 μ.—246–247. Cf. Haloragidaceae, e.g., *Proserpinaca*, 8-1, T-25, 27 μ.—248–255. Cf. Sterculiaceae.—248. 34-1, Q-46,4, 27 μ.—249. 34-1, L-30,1-3, 27 μ.—250–251. 10-1, J-14,1, 30 μ.—252–253. 8-1, U-36,2, 25 μ.—254–255. 25-1, U-41,2-4, 23 μ. [The numbers following plant names represent sample and number, England Slide Finder coordinates, and size.]

likely that climates in southeastern Mexico during the upper Miocene were cooler (e.g., more temperate and seasonal), and with possibly increased or more uniformly distributed rainfall than in the present warm inter-glacial environments.

In discussing the upper Miocene character of Veracruz communities it is not assumed that all members of the Tropical Rain Forest or vegetation of drier aspect were absent from the region. Vegetational history studies have progressed beyond the point of expecting paleocommunities, especially in areas of significant physiographic relief, to rigidly conform in composition to static geoflora-type assemblages. Elements representing a variety of ecotypes are easily accommodated in the topographically diverse region of southern Veracruz. The manner in which these various elements coalesce to form communities, the composition of these communities, and the areal extent they occupy depends on the existing set of environmental conditions and the vicissitudes of seed availability. Within pollen transport range of the Paraje Solo depositional environment, temperate communities during the upper Miocene were well developed in comparison to the tropical and more arid vegetation that presently characterizes the area.

Similarly, the paleoenvironments reconstructed to account for these differences between fossil and modern vegetation involve a complex mosaic of interrelated factors. In addition to a cooler, more seasonal climate it is likely that the higher sea levels of upper Miocene time, prior to the wide-spread development of continental ice sheets, inundated portions of the Veracruz lowland and physically reduced the area available to rain forest development.

These considerations emphasize the dynamic aspect of vegetation and are important concepts in understanding the geologic evolution of communities. Of particular interest is the recent change in view concerning the "stability" of the Tropical Rain Forest. Considering the lowland habitat of sizable portions of the Neotropical rain forest, with its susceptibility to changes in sea level, it may be that this community is actually a delicately balanced ephemeral assemblage that has undergone greater changes in range and composition during the later Cenozoic than more northern temperate biotas closer to the glacial boundary.

Literature Cited

Axelrod, D. I. 1975. Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. Ann. Missouri Bot. Gard. 62: 280–334.

Berry, E. W. 1923. Miocene plants from southern Mexico. Proc. U.S. Natl. Mus. 62: 1–27.

Breedlove, D. E. 1973. The phytogeography and vegetation of Chiapas (Mexico). Pp. 149–165, *in* Alan Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Scientific Publ. Co., Amsterdam. 393 pp.

Clausen, R. T. 1959. *Sedum* of the Trans-Mexican Volcanic Belt. Cornell Univ. Press, Ithaca. 380 pp.

Cohen, A. D. & W. Spackman. 1972. Methods in peat petrology and their application to reconstruction of paleoenvironments. Bull. Geol. Soc. Amer. 83: 129–142.

Deevey, E. S. 1949. Biogeography of the Pleistocene. Bull. Geol. Soc. Amer. 60: 1315–1416.

Flint, R. F. 1971. Glacial and Quaternary Geology. John Wiley, New York. 892 pp.

Flores Mata, G., J. Jiménez López, X. Madrigal Sánchez, F. Moncayo Ruiz, F. Takaki Takaki. 1971. Tipos de Vegetación de la Republica Mexicana. Escala 1:2,000,000. SRH, Dirección de Agrologia, México, D. F.

García, E. 1970. Los climas del estado de Veracruz. Anales Inst. Biol. Univ. Nac. México 41: 3–42.

Garner, H. F. 1974. The Origin of Landscapes. Oxford Univ. Press, London. 734 pp.

Gentry, H. S. 1972. The Agave Family in Sonora. Agriculture Handbook No. 399. U.S. Dept. Agriculture, Washington, D.C. 195 pp.

Germeraad, J. H., C. A. Hopping & J. Muller. 1968. Palynology of Tertiary sediments from tropical areas. Rev. Palaeobot. Palynol. 6: 189–348.

Gómez-Pompa, A. 1966. Estudios botánicos en la región de Misantla, Veracruz. Inst. México Resursos Naturales Renovables, México, D. F. 173 pp.

———. 1973. Ecology of the vegetation of Veracruz. Pp. 73–148, *in* Alan Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Scientific Publ. Co., Amsterdam. 393 pp.

———, L. Hernández Pallares & M. Sousa Sánchez. 1964. Estudio fitoecológico de la cuenca intermedia del Río Papaloapan. Publ. Espec. Inst. Nac. Invest. Forest. México 3: 37–90.

——— & J. M. León Cázares. 1970. Mapas de vegetación en zonas calidas y su importancia. Bol. Espec. Inst. Nac. Invest. Forest. México 5: 1–11.

——— & L. I. Nevling. 1970. La flora de Veracruz. Anales Inst. Biol. Univ. Nac. México 41: 1–2.

Gordon, A. G. 1968. Ecology of *Picea chihuahuana* Martinez. Ecology 49: 880–896.

Graham, A. 1972. Some aspects of Tertiary vegetational history about the Caribbean Basin. Mem. Symp. I Congr. Lationamér. Bot. Pp. 97–117. Sociedad Botánica México, S.A.

———. 1973. History of the arborescent temperate element in the Latin American biota.

Pp. 301–314, *in* Alan Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Scientific Publ. Co., Amsterdam. 393 pp.

———. 1975. Late Cenozoic evolution of tropical lowland vegetation in Veracruz, Mexico. Evolution 29: 723–735.

GRAY, J. 1960. Temperate pollen genera in the Eocene (Claiborne) flora, Alabama. Science 132: 808–810.

———. 1965. Techniques in Palynology. Pp. 471–706, *in* B. Kummel & D. Raup (editors), Handbook of Paleontological Techniques. Freeman & Co., San Francisco.

HAFFER, J. 1969. Speciation in Amazonian forest birds. Science 165: 131–137.

———. 1970. Geologic-climatic history and zoogeographic significance of the Urara region in northwestern Colombia. Caldasia 10: 603–636.

———. 1974. Avian Speciation in tropical South America. Publ. Nuttall Ornithological Club No. 14. Cambridge, Massachusetts. 390 pp.

KENNETT, J. P. & N. J. SHACKLETON. 1975. Laurentide ice sheet meltwater recorded in Gulf of Mexico deep-sea cores. Science 188: 147–150.

LANGENHEIM, J. H., B. L. HACKNER & A. BARTLETT. 1967. Mangrove pollen at the depositional site of Oligo-Miocene amber from Chiapas, Mexico. Bot. Mus. Leafl. 21: 289–324.

LEÓN CÁZARES, J. M. & A. GÓMEZ-POMPA. 1970. La vegetación del sureste de Veracruz. Bol. Espec. Inst. Nac. Invest. Forest. México 5: 13–48.

LEOPOLD, A. S. 1950. Vegetation zones of Mexico. Ecology 31: 507–518.

MALDONADO-KOERDELL, M. 1950. Los estudios paleobotánicos en México, con un catálogo sistemático de sus plantas fósiles. Bol. Inst. Geol. Univ. Nac. México 55: 1–72.

MARTÍNEZ, M. 1963. Las Pináceas Mexicanas. Ed. 3 Univ. Nacional Autónoma de México, México, D. F. 400 pp.

MIRANDA, F. 1963. Two plants from the amber of the Simojovel, Chiapas, Mexico, area. J. Paleontol. 37: 611–614.

MULLERRIED, F. K. G. 1938. Informe del Sr. . . . paleontologo del Instituto de Geología, acerca del material colectado en el municipio de Tlacolulan, estado de Veracruz. Bol. Soc. Geol. México 10: 203–206.

RZEDOWSKI, J. 1961. Vegetación del estado de San Luis Potosí. Tesis Doctoral, Univ. Nac. México, Facultad de Ciencias, México, D. F. 228 pp.

——— & R. MCVAUGH. 1966. La Vegetación de Nueva Galicia. Contr. Univ. Michigan Herb. 9: 1–123.

SALAS, G. P. (Presidente; S. Hernandez Sánchez Mejoroda, Editor). 1968. Carta Geologica de la Republica Mexicana. Escala 1: 2,000,000. México, D. F.

SCHOLL, D. W. 1964a. Recent sedimentary record in mangrove swamps and rise in sea level over the southwestern coast of Florida, Part I. Marine Geol. 1: 344–366.

———. 1964b. Recent sedimentary record in mangrove swamps and rise in sea level over the southwestern coast of Florida, Part II. Marine Geol. 2: 343–364.

SHREVE, F. & I. WIGGINS. 1964. Vegetation and Flora of the Sonoran Desert. 2 vols. Stanford Univ. Press, Stanford, Calif. 1740 pp.

SOUSA, M. 1968. Ecología de las leguminosas de Los Tuxtlas, Veracruz. Anales Inst. Biol. Univ. Nac. México 39: 121–160.

VANZOLINI, P. E. 1973. Paleoclimates, relief, and species multiplication in equatorial forests. Pp. 255–258, *in* B. Meggers, E. S. Ayensu & W. D. Duckworth (editors), Tropical Forest Ecosystems in Africa and South America: A Comparative Review. Smithsonian Inst. Press, Washington, D.C. 350 pp.

——— & E. E. WILLIAMS. 1970. South American Anoles: the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). Arq. Zool. São Paulo 19: 1–240.

VÁZQUEZ, C. 1971. La vegetación de la laguna de Mandinga, Veracruz. Anales Inst. Biol. Univ. Nac. México 42: 49–94.

VUILLEUMIER, B. S. 1971. Pleistocene changes in the fauna and flora of South America. Science 173: 771–780.

ORIGIN OF THE CREOSOTE BUSH (*LARREA*) DESERTS OF SOUTHWESTERN NORTH AMERICA[1]

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ABSTRACT

The North American creosote bush (*Larrea tridentata*) has undergone a simple cytogeographic differentiation, with the ancestral diploid population in the Chihuahuan Desert, and with tetraploid and hexaploid derivatives in the Sonoran and Mohave Deserts, respectively. The chromosomal races have annectant but largely allopatric distributions, which coincide remarkably well with the boundaries of their respective desert provinces. However, during the glacials of the Pleistocene, the lowlands of these provinces were extensively invaded by evergreen woodlands dominated by various species of *Juniperus*, *Pinus*, and *Quercus*; and the generality of the phenomenon during the Wisconsin glacial has been abundantly documented by some of the most detailed macrofossil evidence of relatively xerophytic plants ever obtained. The ^{14}C-dated macrofossil assemblages, preserved in rock-sheltered *Neotoma* deposits, demonstrate a persistence of woodland conifers and consistent absence of *Larrea* throughout most of its present range in the Southwest during the last major glacial episode of the Pleistocene from > 40,000 BP to about 11,000 BP. The oldest reliable record of *Larrea* in North America is dated on macrofossils of *Larrea* itself at 10,580 BP, and the site, near Wellton, Yuma County, Arizona, is one of the lowest (162 m) and most arid in the present Sonoran Desert. Hence, the major features of the modern geographic pattern of *Larrea tridentata* in North America must have originated during the climatic transition from the late Wisconsin to the Holocene, when a desiccating climate gripped the immense lowlands of the Southwest, opening a vast and varied desert niche into which a burgeoning population of *Larrea* could have expanded and differentiated explosively.

The biogeography of *Larrea* during the Pleistocene is a particularly interesting enigma because there is an intriguing possibility of a late, intercontinental dispersal from South America, where the genus exhibits markedly greater ecomorphological and chemical diversity than it does in North America. Also, the genera most closely allied to *Larrea* are endemic to South America. While several "r"-selected, herbaceous genera of Zygophyllaceae have much wider world-distributions, *Larrea* is unique among woody Zygophyllaceae in having an amphitropical, intercontinental disjunction in its range. The specialization of *Larrea* on intensely arid deserts with relatively open plant communities would facilitate establishment after dispersal to a new desert area. However, the migration of *Larrea* to North America must have lacked continuity. If the extremely xerophytic species, *Larrea divaricata*, had been able to follow a hypothetically continuous route across the wet tropics during a period of drier climate, then a much greater amphitropical disjunction of American zygophyllaceous genera should be expected. Long distance transport of seeds across the wet tropics is the only feasible alternative for *Larrea*.

The creosote bush [*Larrea tridentata* (Sessé & Moc. ex DC.) Cov.] is the most abundant and widely distributed woody plant in the warm or subtropical deserts of North America. It forms a massively continuous population throughout the Mohave Desert and the Colorado River sector of the Sonoran Desert, and extends eastward on the more arid plains to the "desert grasslands" of southeastern

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FIGURE 1. Distribution of the warm, subtropical, and tropical deserts of North and Middle America: (1) *Mohavean*. (2) *Sonoran* (including the shaded areas in southern Baja California and southern Sonora). (3) *Chihuahuan*. (4) *Hidalgan* (Río Extorax, Querétaro, to northwest; Valle del Mezquital, Hidalgo, to southeast). (5) *Pueblan* (Valle de Tehuacán, Puebla, to northwest; Valle de Tomellín, Oaxaca, to southeast). (6) *Guatemalan* (Valle de Chixoy to west, Valle de Motagua to east). Shaded areas in the southern Sonoran Desert and the tropical, rain-shadowed, pockets of aridity (desert "islands," numbered 4, 5 and 6) were probably full-glacial, Pleistocene refugia for thermophilous desert xerophytes, but possibly not for *Larrea*. *Larrea* is lacking in areas 5 and 6, which are dominated by dense, thorn woodland or shrubland with gigantic cacti. Cytogeographically, *Larrea tridentata* is hexaploid in desert area (1); tetraploid in area (2); diploid in areas (3) and (4) and also throughout the range of its counterpart in South America. Localities for Pleistocene *Neotoma* records of pluvial woodland within the present range of *Larrea* are marked by large dots (map compiled and annotated by P. V. Wells).

Arizona and southern New Mexico, and again dominantly and continuously throughout the Chihuahuan Desert to its southern extremity south of the Tropic of Cancer (Fig. 1). Thus, the creosote bush extends from southern California and southwestern Utah, south through Baja California and Sonora, and southeastward through western Texas, Chihuahua, Coahuila and San Luis Potosí (Shreve, 1942; Rzedowski & Medellín Leal, 1958; Wells, 1977). There is a major disjunction for more than 100 km to the southeast of San Luis Potosí, which isolates a substantial population of *L. tridentata* on the Extorax-Tula drainage of eastern Querétaro from the main body of *Larrea* to the north; and a small colony or two occurs in

the Valle del Mezquital (Rzedowski & Medellín Leal, 1958) on another branch of the same drainage system in Hidalgo, just north of Mexico City (Fig. 1). Aside from these disjunct populations in the south, and a patchy distribution in the desert grasslands, the North American creosote bush is very nearly one continuous population, extending over many millions of square kilometers in more or less pure stands. Nevertheless, there has been a remarkable cytological differentiation, and some parallel morphological variations within this wide geographic range; *Larrea* exists as distinct, diploid ($n = 13$), tetraploid ($n = 26$), and hexaploid ($n = 39$) cytogeographic races in the Chihuahuan, Sonoran, and Mohave deserts, respectively (Yang, 1967, 1968, 1970; Barbour, 1969).

The strikingly annectant, though largely allopatric, distributional areas of the three chromosomal races are nearly congruent with the boundaries of their respective deserts, but all of these existing areas of desert vegetation are now known to have undergone extensive geographical changes during the Pleistocene. Most of the present areas of the warm deserts in North America were occupied by pluvial woodlands dominated by low, xerophytic evergreen trees, with various species of junipers (*Juniperus*), and to some extent pinyon pines (*Pinus*) and oaks (*Quercus*), segregating geographically among the Mohave-Sonoran and Chihuahuan desert provinces (Wells, 1966, 1969, 1977; Wells & Berger, 1967; Van Devender, 1973). The woodlands persisted in what are now desert lowlands until the waning phases of the Wisconsin glacial, beginning to decline perhaps as early as about 12,000 years ago at low elevations (< 600 m) in the subtropical latitudes of the Chihuahuan and Sonoran deserts, but lingering until about 9,000 BP or less at the higher elevations generally (> 1000 m) of the northerly and winter-cold Mohave Desert (Wells, 1977). Hence, the present distributional range of *Larrea* in North America appears to be recent.

Indeed, the sharply delineated spatial pattern of its polyploid races (Yang, 1970) strongly suggests that the cytogeographic differentiation of *Larrea* in the North American deserts has developed *pari passu* with a northwestward migration from southern Mexico, the most likely Ice Age refugium for the ancestral diploid, or perhaps its original point of immigration from South America (see below). Since there is no evidence for more than one species of *Larrea* in North America, the doubling and tripling of its chromosome number amounts to autopolyploidy. Investigations of protein spectra, acid-soluble phenolics, and cuticle resins of *Larrea* all indicate a rather uniform chemistry for the three cytological races that are segregated among the major deserts of the Southwest (Hunziker et al., 1972; Mabry et al., 1977). The data suggest interracial autoploidy. The Mohavean hexaploid could have been derived from a combination of reduced and unreduced gametes due to meiotic irregularity in the Sonoran tetraploid at the cooler and drier northwestern limits of its range. Although the possibility of an earlier cycle of expansion of the creosote bush deserts (followed by contraction to one or more refugia during the last glacial, and by reexpansion during the Holocene) cannot be ruled out on the present evidence, it seems unlikely that the remarkably simple existing cytogeography and chemistry of *Larrea* in North America could stem from so complicated a history.

OLDEST RECORDS OF *LARREA* IN NORTH AMERICA

The major features of the modern geographic pattern of *Larrea* on this continent probably originated during the climatic transition from the late Wisconsin glacial to the Holocene, when a desiccating climate gripped the immense lowlands of the Southwest, opening a vast and varied desert niche into which a burgeoning population of *Larrea* could have expanded and differentiated explosively. The oldest, well-documented record of *Larrea* in North America is dated at 10,580 ± 550 BP. The radiocarbon age was determined on macrofossils of *Larrea tridentata* itself, preserved in an ancient, rock-sheltered *Neotoma* (wood rat) midden from the Wellton Hills, east of Yuma in southwestern Arizona, at the very low elevation of 162 m (Van Devender, 1973). The deposit contains a desert assemblage similar to the xerophilous Sonoran Desert scrub presently growing at the site, except for the abundant macrofossils of an *Ephedra* which is now absent from the immediate area. An early occurrence of desert conditions slightly different from today seems to be established. However, other deposits obtained by Van Devender (1973) at the same locality have a similar content of *Larrea* and *Ephedra*, but have yielded much younger dates, ranging from 6,600 ± 370 to 7,950 ± 370 BP on *Larrea* macrofossils, and from 8,150 ± 260 to 8,750 ± 320 BP on *Ephedra* macrofossils. The predominance of younger dates suggests that the entire series of deposits from the Wellton Hills is early Holocene in age. If the 10,580 BP date (A-1407) is indeed accurate, it indicates an early onset of modern desert conditions at a very low elevation in one of the most arid sectors of the Sonoran Desert.

On the other hand, there are 26 dated *Neotoma* records from the lowlands of the Sonoran Desert that document the prevalence of pluvial woodlands dominated by *Juniperus*, but with no trace of *Larrea*, during the Wisconsin glacial from about 10,000 to > 38,000 BP (Wells, 1977). The pluvial, juniper *sans* creosote-bush woodland is recorded throughout the Sonoran Desert, even in the southern sector, and at elevations ranging from about 600 m down to about 260 m, less than 100 m above the Wellton Hills site (at 162 m). Although the latter site has been regarded as a refugium for the *Larrea* desert during the Wisconsin glacial (Van Devender, 1973), the *Neotoma* deposits are too young to prove the point. The strong positive evidence for a widespread occurrence of pluvial woodlands in the Sonoran Desert complements the negative evidence on *Larrea* (Table 1). It should be pointed out that negative *Neotoma* evidence on a potentially dominant element of the vegetation, like *Larrea*, is a fairly robust indication, so assiduous are the wood rats at collecting detailed inventories of the local flora (Wells, 1976). An authenticated contemporaneity of *Larrea* and *Juniperus* has proven to be elusive in Ice Age middens of *Neotoma*, despite the fact that modern examples of this combination are not uncommon within the narrow elevational overlap of these outstanding zonal dominants. Furthermore, *Larrea* has contributed abundantly to the ubiquitous Holocene *Neotoma* middens at desert elevations in the Southwest, amply demonstrating a lack of bias against *Larrea*. The few instances of commingling of *Larrea* and *Juniperus* macrofossils in Pleistocene wood rat deposits are apparently due to redeposition. For example, one

TABLE 1. Oldest *Neotoma* records of *Larrea* in North America are compared to records of *Juniperus*, with the sites arranged in 3 increments of elevation. *Larrea* replaced *Juniperus* as early as 10,500 BP, but only at the lowest elevation range of the subtropical Sonoran Desert. *Juniperus* persisted as late as 8,400 BP at higher elevations, especially in the winter-cold Mohave Desert. Thus, the early Holocene, cliseral transition from *Juniperus* (or pinyon-juniper) woodland to *Larrea* desert in the lowlands of the Southwest was time transgressive. References are: (1) Mehringer & Hooke (1969). (2) Van Devender (1973). (3) Wells & Berger (unpublished). (4) Wells & Berger (1967). (5) Van Devender & King (1971). (6) Wells & Jorgensen (1964).

Site	Desert	Elevation (m)	^{14}C Date, BP	Macrofossils		Reference
				Larrea	*Juniperus*	
Low-Elevation Range (0–500 m)						
Death Valley, Calif.	Mohave	–73	990 ± 110	abundant	nil	(1)
Wellton Hills, Ariz.	Sonoran	162	6,600 ± 370	abundant	nil	(2)
Wellton Hills, Ariz.	Sonoran	162	7,950 ± 370	abundant	nil	(2)
Wellton Hills, Ariz.	Sonoran	162	10,580 ± 550	abundant	nil	(2)
Chemehuevi Mt., Calif.	Sonoran	258	16,900 ± 190	nil	abundant	(3)
Central Sonora	Sonoran	457	> 38,000	nil	abundant	(3)
Mid-Elevation Range (500–1,000 m)						
New Water Mt., Ariz.	Sonoran	603	2,710 ± 280	abundant	nil	(2)
Newberry Cave, Calif.	Mohave	670	7,400 ± 100	abundant	nil	(4)
N. Muddy Mt., Nev.	Mohave	555	9,900 ± 100	nil	abundant	(3)
Artillery Mt., Ariz.	Sonoran	615	10,250 ± 200	nil	abundant	(5)
New Water Mt., Ariz.	Sonoran	603	11,000 ± 505	nil	abundant	(2)
Shit House Mt., Ariz.	Sonoran	551	11,450 ± 400	nil	abundant	(2)
N. Muddy Mt., Nev.	Mohave	533	17,750 ± 200	nil	abundant	(4)
Turtle Mt., Calif.	Sonoran	850	19,500 ± 380	nil	abundant	(4)
High-Elevation Range (1,000–2,000 m)						
Spotted Range, Nev.	Mohave	1830	8,420 ± 100	nil	abundant	(4)
Mercury Ridge, Nev.	Mohave	1390	9,000 ± 250	nil	abundant	(6)
Lucerne Valley, Calif.	Mohave	1070	9,140 ± 140	nil	abundant	(4)
Aysees Peak, Nev.	Mohave	1525	9,320 ± 300	nil	abundant	(6)
Spotted Range, Nev.	Mohave	1550	9,450 ± 90	nil	abundant	(4)
Ranger Mt., Nev.	Mohave	1100	10,100 ± 160	nil	abundant	(6)
Ranger Mt., Nev.	Mohave	1100	17,450 ± 300	nil	abundant	(6)

Neotoma deposit from an arid sector of the Sonoran Desert in Yuma County, Arizona, contained *Larrea* together with juniper and oak. However, monospecific dating of separated macrofossils of the different species gave a radiocarbon age of only 2,710 ± 280 BP (late Holocene) for the *Larrea*, in contrast to 11,000 ± 505 BP (late Wisconsin) for the *Juniperus* (Van Devender, 1973).

The exact time of onset of desert conditions in the lowlands of the Southwest is not known, but a shift to drier climate may be inferred from compositional changes in the youngest series of *Neotoma* deposits in Maravillas Canyon, Texas, which at 600 m is close to the minimal elevation for the entire Chihuahuan Desert province, and lies 800 m below existing woodland. One thick sequence has a basal layer with a radiocarbon age of 12,550 ± 130 BP. The layer contains a rich assemblage of woodland species, with relatively more pinyon pine and juniper than scrub oak, and it has comparatively few "desert" species. Moreover, the composition of this deposit is essentially the same as nearby deposits of more or less full-glacial age (14,800 ± 180, 16,250 ± 240, and 20,000 ± 390 years BP) at the same elevation (600 m) or even higher (880 m). Hence, climatic conditions equivalent to the maximal pluvial effects of the Wisconsin glacial in the Chihuahuan Desert region were still in force there at the lowest elevations about 12,500 years ago (Wells, 1966).

In contrast, the two younger deposits in normal superposition in the series, with radiocarbon ages of 12,000 ± 150 and 11,560 ± 140 years BP, have much more scrub oak and juniper than pinyon pine, and contain several "desert" or semidesert species lacking in older deposits (but no *Larrea*): *Acacia roemeriana* Scheele (armed shrub); *Yucca rostrata* Engelm. and *Y. torreyi* Shafer (semisucculent rosette shrubs); *Echinocereus* cf. *dasyacanthus* Engelm. (stem succulent). These changes clearly indicate that the climate already had begun to warm or to desiccate about 12,000 years ago, and this trend was still continuing about 11,500 years ago. It is as yet uncertain whether the apparent lack of further deposition by wood rats, immediately after 11,500 years ago, signifies the termination of pluvial woodland climate in the lowlands of the Chihuahuan Desert at about that time. Since *Larrea* now grows abundantly near this and other ancient *Neotoma* sites in the deserts of the Southwest, its consistent absence in deposits older than 8,000–10,000 BP is compelling, even though negative, evidence (Table 1).

Full-Glacial Displacement of Woodlands into the Warm Deserts of North America

The pluvial woodlands that occupied what is now the *Larrea* zone left an abundant macrofossil record in numerous Pleistocene *Neotoma* middens sheltered in dry caves throughout the Southwest. The greatly expanded Pleistocene woodlands varied geographically in species composition, as do the drastically shrunken modern remnants that have retreated upward 600–800 m or more to the relatively restricted areas of higher elevation (Wells, 1969). In the more arid, orographic rain shadows of the Mohave Desert region, a well-marked, late-Pleistocene zonation was developed within the woodland zone, as follows: (1) Higher elevations: *Pinus monophylla* Torr. & Frém. (single leaf pinyon), *Juni-*

perus osteosperma (Torr.) Little (Utah juniper), *Acer glabrum* Torr. (a xerophytic maple), *Ceanothus greggii* A. Gray (an evergreen sclerophyll of chaparral), *Chamaebatiaria millefolium* Maxim. (fern bush). (2) Lower elevations: *Juniperus osteosperma*, *Yucca brevifolia* Engelm. (Joshua tree), *Y. whipplei* Torr. (Our Lord's candle, now extinct in the Mohave Desert), *Atriplex confertifolia* S. Wats. (shadscale), and other desert shrubs, but never *Larrea* (Wells & Jorgensen, 1964; Wells & Berger, 1967, unpublished; Wells, 1977).

The lower part of the juniper-Joshua tree zone extended from the eastern Mohave Desert south along the trough of the lower Colorado River valley into what is now the northwestern Sonoran Desert, descending to an elevation of 260 m, and possibly lower (Wells & Berger, 1967; Wells, 1972, 1977; Van Devender, 1973; Phillips & Van Devender, 1974). A *Neotoma* midden with the xerophilous juniper-Joshua tree woodland assemblage of macrofossils, but without a trace of *Larrea*, was found at the latter elevation between Needles and Parker in the midst of the extremely arid *Larrea* zone of the Colorado sector of the Sonoran Desert. The deposit has a radiocarbon age of 16,900 ± 190 BP (UCLA-1666), which is equivalent to full-glacial age. Presence of *Juniperus* and absence of *Larrea* is also recorded in *Neotoma* deposits (one dated at > 38,000 BP) from the low plains (450 m) of the southern Sonoran Desert in the latitude of Hermosillo, Sonora (29° N), an area now dominated by saguaro-paloverde/creosote-bush desert, and lacking mountains high enough to support *Juniperus* at present (Wells & Berger, unpublished).

The higher elevation zone of the pluvial woodlands of the Mohave region also occurred in the mountains along the northwestern fringe of the Sonoran Desert province in southeastern California and western Arizona. Thus, *Pinus monophylla* and *Juniperus osteosperma* dominated the long-vanished, pluvial pinyon-juniper zone of the now arid Turtle Mountains, being recorded at about 14,000 BP in *Neotoma* middens as low as 730 m, in what is now paloverde-ironwood/creosote-bush desert (Wells & Berger, 1967). From the lower Colorado River valley eastward across the Sonoran Desert, shrubby live oaks (*Quercus turbinella* Greene, *Q. palmeri* Engelm.) were important associates of the pluvial woodland conifers at elevations above 600 m (Leskinen, 1970; Van Devender & King, 1971; Van Devender, 1973), just as they are today at much higher elevations along the Mogollon Rim and in the mountains of northwestern Arizona and southern Nevada. The Pleistocene *Neotoma* records of live oaks from southwestern Arizona, dated as recent as about 11,000 BP, are supplemented by relictual colonies of a shrubby, xerophytic oak (*Q. turbinella* with some characters of *Q. ajoensis* C. H. Muller), surviving to the present day in deep, mesic canyons of the low and isolated Shit House and Castle Dome mountains (Tucker & Muller, 1956). The latter ranges are remarkable in still harboring a live-oak, while becoming too arid to support the xerophilous conifers of the pinyon-juniper woodland, which formerly associated with it in this sector of the Sonoran Desert (e.g., in the Shit House Mountains at 862 m, about 13,000–14,000 BP). Presence of evergreen oaks in the pluvial woodlands at higher elevations of what is now the Sonoran Desert suggests a mild climate there during the glacials of the Pleistocene.

Far to the southeast, this trend was developed to a greater degree in the Big Bend area of the Chihuahuan Desert, with a different set of evergreen oaks (*Quercus pungens* Liebm., *Q. grisea* Liebm., *Q. arizonica* Sarg.) sorting out in Wisconsin-age *Neotoma* middens throughout the range of elevation of the existing desert, together with the different pinyon pine (*Pinus cembroides* Gord.) and junipers (*Juniperus pinchotii* Sudworth, *J. deppeana* Steud.) of the region (Wells, 1966). Hence, the pluvial woodlands of the Chihuahuan Desert province differed significantly from those of the Sonoran and Mohave desert provinces in having a much lesser degree of zonation with elevation (that is, no evidence of downward segregation of a pineless, oakless, juniper zone). In fact, the full-glacial *Neotoma* record shows a uniform dominance of pinyon, juniper, and scrub live-oak over the entire span of elevation available in the Chihuahuan Desert (Wells, 1977). Again, as in the other deserts now dominated by the creosote bush, no trace of *Larrea* was detected in the pluvial-age *Neotoma* deposits (Wells, 1966). Absence during the Wisconsin glacial of segregated *Juniperus*, *Juniperus-Yucca*, or *Yucca* zones at lower elevations in the northern Chihuahuan Desert stands in striking contrast with the very characteristic zone of arborescent yuccas and other Agavaceae within and just below the montane woodlands in the province today (Wells, 1965). The lack of zonation, and the consistent presence of evergreen oaks, indicate that the Chihuahuan Desert province enjoyed an even more mesic, pluvial woodland climate in its vast, now arid lowlands than the Sonoran Desert, which, in turn, was probably more equable (mild, even climate) than the cool-arid, oakless, Mohavean province to the northwest. The apparent east-west, paleoclimatic gradient of increasing aridity in the lowlands during the Wisconsin glacial may have been caused by decreasing summer rainfall in the westward direction, as a function of decreasing penetration of moist air masses with increasing distance from the Gulf of Mexico, essentially as in the modern pattern.

Full-Glacial Refugia for Warm-Desert Species

The decidedly high elevation (1,500–2,300 m) of the *Larrea* plains in the southern sector of the Chihuahuan Desert in Zacatecas and San Luis Potosí would seem to render them even less suitable as warm-desert refugia under the full-glacial climate than the low elevation (600–1,400 m) trough along the Río Grande. The strongly meridional atmospheric circulation during the glacials would have greatly augmented the present wintry visitations of rainy or snowy cold fronts caused by outbreaks of polar air from the north (the *norte*, or norther), which would have had a telling effect on thermophilous desert vegetation at such high elevations. Moreover, the 800 m pluvial downward displacement of the pinyon-juniper-oak woodland zone, firmly established by abundant macrofossil evidence in the much lower and presently hotter and more arid Big Bend area of the Río Grande valley (Wells, 1966), would have been more than enough to shift the main body of the woodland zone down onto the high intermountain plateau of the southern Chihuahuan Desert province (Wells, 1977).

Where then did the floristically rich, warm deserts survive the glacials of the Pleistocene? Suitable full-glacial refugia for the extremely xerophytic, thermo-

philous desert vegetation of North America might be sought where there is a combination of low elevation, tropical latitude, orographic rain shadow (also providing protection from outbreaks of polar air), and therefore local or regional aridity, well buffered against pluvial invasion by more competitive, mesophytic trees and shrubs. One example might be the arid, rain-shadow pocket on the Extorax-Tula drainage in eastern Querétaro at 21° N, which now harbors a remarkably isolated area of *Larrea*-dominated landscape at elevations ranging from 1,000 m or less to about 1,500 m (northwestern sector of desert "island," numbered 4 in Fig. 1). A significantly large number of Chihuahuan Desert species are known to share this distribution. For example, Quintero (1968) lists 47 species in 34 genera that are important elements of the Chihuahuan Desert vegetation, and which occur in the Valle del Mezquital, Hidalgo (southeastern part of desert "island," Fig. 1, number 4). These include *Larrea*, *Flourensia cernua* DC., *Euphorbia antisyphilitica* Zucc., and *Agave lecheguilla* Torr. Hence, the flora of the Chihuahuan Desert has extended into this southeasterly pocket in full force.

The mild but arid climate in Querétaro and Hidalgo is reflected in the rich diversity of succulents, including about 18 genera and 77 species of cacti (Bravo, 1936; 1937; Britton & Rose, 1920). The fact that many of the cacti are narrowly endemic within this limited area strongly suggests a considerable antiquity for the desert plants confined there. The endemics almost certainly antedate the later glacials of the Pleistocene, but did they evolve *in situ*? In this connection, there are several species of large, temperature-sensitive cacti in the same area, namely the columnar *Cephalocereus senilis* Pfeiff. (endemic) and *Pachycereus marginatus* Britton & Rose (endemic); the gigantic, candelabriform *Lemaireocereus dumortieri* Britton & Rose and *Myrtillocactus geometrizans* Cons.; and enormous barrel cacti of the genus *Echinocactus*. Large, succulent cacti are known to be extremely sensitive to frost (Shreve, 1951). The relatively hardy saguaro (*Carnegiea gigantea* Britton & Rose), which has the most northerly distribution of any of the columnar giants of México, is nevertheless subject to damage from frost in Arizona if temperatures drop below –5° C for a brief period, and death may result from exposure to frost (0° C) for 29 consecutive hours (Shreve, 1911). It may be inferred that the giant succulents of southern Mexico are at least as good indicators of mild winter climate as the saguaro, and that the narrowly endemic columnar or candelabriform giants are located in areas that have not been subjected to severe frost during their long tenure. Hence, it seems very likely that the lower elevation range of the Querétaro-Hidalgo rain-shadow pocket had a relatively mild, frost-free climate during the glacials of the Pleistocene. At the same time, the climate must have been arid enough to harbor the rich and partly endemic assemblage of xerophytes presently sequestered there, inasmuch as the rain-shadow is an isolated cul-de-sac, and there is no lower or drier area available which could have served as a better refugium for the desert flora. At lower elevations, the Río Tula drainage cuts through the Sierra Madre Oriental and enters a much wetter climate with dense, nondesert vegetation.

There are a few other rain-shadow deserts in southern Mexico and Guatemala (see Fig. 1), and no other desert in North America is richer in bizarre xerophytes

than the Valle de Tehuacán, Puebla, with about 9 genera and 24 species of gigantic cacti. However, each of these islandlike pockets of aridity has its own unique assemblage of desert plants, and all of the deserts south of Hidalgo lack *Larrea* (Wells, 1977). Thus, there is no phytogeographic indication of any massive connection of the isolated deserts of Puebla-Oaxaca and Guatemala with the main body of the North American deserts about 500 km or more to the north, even if such a connection were physiographically possible. In fact, the Neovolcanic Axis is studded with lofty volcanos from Volcán Orizaba near the Gulf of Mexico to Volcán Colima near the Pacific coast, and the interconnecting high divides interpose a formidable east-west barrier to the north-south migration of thermophilous desert plants, even now. Of course, vegetation zones were much lowered during the glacials, when the high peaks were glaciated (Flint, 1971), thus enhancing the montane barrier.

The Sonoran Desert was undoubtedly a major desert refugium during the Pleistocene. With 141 families, 731 genera and 2,581 species of vascular plants (Shreve & Wiggins, 1964), the Sonoran Desert has the richest flora of all the deserts in North America, although it is not the most areally extensive of the warm deserts, being exceeded in this respect by the Chihuahuan Desert. The high rate of endemism in the subtropical flora of the Sonoran Desert (about 30% of the 2,581 species are unknown outside its boundaries), and the rich assemblage of cacti (20 genera, 173 species), constitute the best evidence that some areas in the vicinity of the existing desert served as an Ice Age refugium for desert plants. Since the known macrofossil record from southeastern California, southwestern Arizona, central Sonora and northern Baja California documents an extensive incursion of pluvial woodlands throughout the greater part of the northern Sonoran Desert, the refugium was most likely in the southernmost sector, including the southern half of Baja California, the southern extremity of Sonora, and perhaps northern Sinaloa (Fig. 1, shaded area). The desert flora of Baja California, with 1,450 species, comprises more than half (56%) of the flora of the Sonoran Desert, and with 461 endemic species accounts for nearly 60% of the endemism, despite the relatively small area of the peninsula compared to the mainland. Thus, southern Baja Cauifornia has almost certainly been a major refugium for desert xerophytes during at least the Wisconsin glacial. Whether it was a refugium for *Larrea* remains unknown.

ORIGIN OF THE NORTH AMERICAN POPULATION OF *LARREA*

The biogeography of *Larrea* during the Pleistocene is a particularly interesting enigma because there is an intriguing possibility of a late, intercontinental dispersal from South America, where the widely disjunct genus exhibits markedly greater morphological and ecological diversity than it does in North America (Hunziker et al., 1972). There are four very different species of *Larrea* in South America, but only one species is present in North America, namely, *L. tridentata* (Sessé & Moc. ex DC.) Cov., which is evidently a derivative of the South American *L. divaricata* Cav. The two very similar taxa have been regarded as conspecific, the North American one being *L. divaricata* subsp. *tridentata* (Sessé & Moc. ex DC.) Felger & Lowe.

Among the several lines of evidence supporting a South American origin for the North American population of *Larrea*, the most important phylogenetic point is that two of the endemic South American species occurring in less xeric (and therefore less specialized) habitats in Argentina and Chile, namely *L. ameghinoi* Speg. and *L. nitida* Cav., have multifoliolate, pinnately compound leaves, which are ancestral traits within their family, the Zygophyllaceae. However, the peculiar bifoliolate leaf of the North and South American populations of the more xerophilous *L. tridentata* and *L. divaricata* is reduced to only the basal (?) pair of leaflets of a pinnate leaf. Also, the virtually unifoliolate leaf of the even more xerophilous Argentinan endemic, *L. cuneifolia* Cav., presents a further simplification by partial fusion of the two leaflets. The leaves of *L. cuneifolia* are uniquely specialized in their vertical orientation with respect to the noonday sun, thus reducing insolation in the manner of the well known "compass" plants (e.g. *Silphium laciniatum* L. of the North American prairie). *Larrea divaricata* (s. lat.) and *L. cuneifolia*, with their specialized, reduced leaves, are by far the most xerophytic species in the genus, occurring in some of the most arid deserts in the world, and the latter species occurs in even drier habitats than the former (Hunziker et al., 1972). Thus, *L. cuneifolia* is the xerophytic culmination of an evolutionary reduction series from the relatively mesophytic, multifoliolate, pinnate leaf, with some steps in the pattern surviving today only in South America. Another uniquely South American vegetative character in this genus of erect shrubs is seen in *L. ameghinoi*, which has a prostrate, creeping growth habit, no doubt conferring fitness in its native habitat on the windy plains of Patagonia. It is unlikely that the strikingly ecomorphological phyletic pattern of *Larrea* in South America has evolved as a result of a hypothetical introduction from North America of the evolutionarily advanced taxon, *L. tridentata*, although this is a possibility that has been considered by a respected minority of botanists.

On the other hand, the North American *L. tridentata* has differentiated into a series of polyploid races, diploid ($n = 13$) toward the southeast, and hexaploid about 1,000 km to the northwest (see above), whereas the South American vicariant, *L. divaricata*, is consistently diploid throughout a 2,500 km transect of *Larrea* desert (Hunziker et al., 1972). But the latter taxon has putatively contributed a complement of chromosomes to the genome of the allotetraploid ($n = 26$) South American endemic, *L. cuneifolia*. The natural triploid hybrid between *L. cuneifolia* and the diploid, South American *L. divaricata* formed 13 bivalents + 13 univalents in nearly 50% of the pollen mother cells examined (Hunziker et al., 1972). Hence, *L. divaricata*, despite its apparent lack of *infraspecific* cytological differentiation, must be a more ancient resident of South America than its alloploid offshoot, *L. cuneifolia*, the most xerophytic, and perhaps the most evolutionarily advanced, member of the genus *Larrea*. The striking cytogeographic differentiation within the North American *L. tridentata*, together with the complete distinctness of the insect faunas on *Larrea* in North and South America (C. D. Michener, personal communication), suggest that *Larrea* is also of some antiquity on the North American continent (Turner, 1972; Porter, 1974). However, electrophoretic analyses of proteins (seed albumins),

paper chromatography of acid-soluble phenolic compounds, and chemical analyses of phenolic, cuticle resins establish a uniform chemistry throughout the geographically extensive, cytologically differentiated populations of *L. tridentata* in North America (Hunziker et al., 1972; Mabry et al., 1977). These data suggest an autoploid, and probably recent, origin for the cytogeographic races of *L. tridentata* in North America. The South American species of *Larrea*, including *L. divaricata*, show considerable interspecific and geographic diversity in their chemistry, again indicating a greater antiquity for the genus in South America (Mabry et al., 1977).

Reproductive Strategy and Migration

The biogeography of the other genera in the family Zygophyllaceae offers some perspective on the origin of the enormous disjunction in the distribution of *Larrea*; it should be pointed out that the northernmost outlier population of *L. divaricata* near Ica, Peru (Morello, 1958) is separated by more than 5,000 km of unsuitably humid tropical vegetation from the southernmost outlier population of *L. tridentata* near Ixmiquilpan, Hidalgo, México (Rzedowski & Medellín Leal, 1958), while the main populations are about 7,000 km apart. However, other genera of Zygophyllaceae show even wider disjunctions (Table 2). *Kallstroemia* has 17 species segregated in North and South America, and the related *Tribulopsis* has 7 species in Australia. Both genera relate to the now subcosmopolitan, weedy genus *Tribulus*. *Fagonia* has 9 species in North America, 3 in South America, and 38 in Africa-Eurasia. *Peganum* has 1 species in the Chihuahuan Desert of México and another 2 species in the aridlands of North Africa-Eurasia (Porter, 1974). But *Kallstroemia*, *Tribulus*, *Tribulopsis*, *Fagonia*, and *Peganum* are herbaceous annuals or perennials (or subligneous in many *Fagonia*) of relatively dry, open habitats that have opted for an "r" strategy with a high ratio of reproductive to vegetative effort (Gadgil & Solbrig, 1972). Indeed, *Tribulus terrestris* L. and *Peganum harmala* L. are very weedy herbs, aggressively spreading through the warmer or drier regions of the world. In general, "r"-selected, herbaceous or subligneous species have a well-developed dispersal capacity, which confers fitness by enabling them to invade open habitats that are distant from the parent population and relatively free of intense competition, which favors successful ecesis. The invasive, colonizing way of life, associated with a large reproductive effort and brief longevity, predisposes "r"-strategists to the vagaries of long-distance, even intercontinental, disperal, as in the weedy, light-seeded, wild tobaccos, which have reached North America, and even Australia (cf. *Tribulopsis*) and the South Pacific islands, from their ancestral seat in northern South America (Wells, 1959; Goodspeed, 1954).

In contrast, woody shrubs and trees have a relatively "K" strategy of allocation of photosynthate, assigning a large proportion to vegetative growth (as wood), and producing fewer, relatively heavy seeds with reduced potential for dispersal, but with a greater chance for success at carrying capacity ("K") population-densities. Salisbury (1942) has thoroughly documented the relative seed weights and dispersal capacities of herbs and woody plants (cf. Baker, 1972). The general principle of greater intercontinental dispersal capacity of herbs

TABLE 2. Intercontinental distributions of the American genera of Zygophyllaceae, and some allied genera of South Africa and Australia, with the number of species per continent. Basic chromosome number (x) from literature (largely from Porter, 1972, 1974). Compare the wide, intercontinental disjunctions within herbaceous, "r"-selected genera, and the narrow, continental endemism of woody, relatively "K"-selected genera, with the notable exception of *Larrea*.

Genera	x	N. America	S. America	S. Africa	N. Africa-Eurasia	Australia
Woody:						
Bulnesia	13	0	8	0	0	0
Larrea	13	1	4	0	0	0
Porlieria	13	0	3	0	0	0
Plectrocarpa	13	0	2	0	0	0
Metharme	—	0	1	0	0	0
Pintoa	10	0	1	0	0	0
Guaiacum	13	5	1	0	0	0
Morkillia	—	2	0	0	0	0
Sericodes	15	1	0	0	0	0
Viscainoa	13	1	0	0	0	0
Neoluederitzia	—	0	0	1	0	0
Sisyndite	10	0	0	1	0	0
Herbaceous or subligneous:						
Kallstroemia	16	7	10	0	0	0
Tribulopsis	—	0	0	0	0	7
Fagonia	9–12	9	3	2	36	0
Peganum	11–12	1	0	0	2	0

(more so for annuals than perennials) relative to woody plants is beautifully exemplified by the amphitropical, disjunct distributions in the floras of North and South America. More than 200 species, or vicarious species-pairs, show the amphitropical disjunction, but woody plants and K-selected herbs of closed communities are scarcely represented (Raven, 1963). Significantly, the few woody genera with more or less conspecific, amphitropical disjuncts are desert shrubs of open, readily colonized habitat: *Atamisquea emarginata* Miers and *Koeberlinia spinosa* Zucc., both of the Capparidaceae, and the vicariant pair *Larrea divaricata-L. tridentata*.

On the other hand, *Larrea* is unique among the many woody genera of the xerophytic family Zygophyllaceae in having a major, *intercontinental* disjunction in its range, and doubly so, because the disjunction is due to very closely related, vicariant species. The North American population of *Larrea* is classified as a separate species, *L. tridentata*, but it differs mainly in having acute stipules and somewhat falcate leaflets (Porter, 1963). In the great majority of characters, including a diversity of other vegetative and floral traits, protein spectra, and acid-soluble phenolics, the North American population of *Larrea* parallels the South American species *L. divaricata* (Hunziker et al., 1972). If current studies show that genetic barriers to reproduction exist (experimental hybrids are semisterile), then perhaps *L. tridentata* is properly accorded the rank of semispecies or sibling species with *L. divaricata* (Yang, Hunziker, et al., unpublished). The greater morphological and ecological differentiation of *Larrea* in South America suggests a greater antiquity for the genus in that segment of the disjunction.

The distribution of woody genera even remotely related to *Larrea* is predominantly confined to the two large continents of the southern hemisphere (Table 2). Thus, there are 7 genera and 20 species of woody Zygophyllaceae in South America and 3 monotypic genera in southern Africa; this compares with 5 genera and 10 species in North America. Moreover, the genera closest to *Larrea* are the South American endemics *Metharme* (monotypic) and *Plectrocarpa* (ditypic), according to Engler (1896), who made a comprehensive study of the distribution and systematics of the Zygophyllaceae. The genus *Larrea* has no close relatives in North America, although it shares a few characteristics with the monotypic genus *Sericodes*, an endemic shrub of the Chihuahuan Desert with a deviant karyotype ($n = 15$). *Sericodes* has similar, densely pubescent fruits, dividing into tiny, light, hairy mericarps with a potential for long-distance, ectozoic dispersal, and it may have had a migrational history similar to that of *Larrea*.

Mode of Intercontinental Migration

The weight of biogeographic evidence supports a South American origin for the genus *Larrea*, but the migration to North America must have lacked continuity. If the extremely xerophytic species *Larrea divaricata* had been able to follow the hypothetically continuous route across the now wet tropics (from northern South America through the Central American isthmus to southern Mexico) during a period of drier climate (Johnston, 1940), then a much greater amphitropical disjunction of zygophyllaceous genera should be expected to exist between the deserts of North and South America. As it is, the only real disjunctions are in *Larrea* and *Fagonia* (Porter, 1974). The single species of *Guaiacum* (*G. officinale* L.) reaching South America is a relatively mesophytic, island-hopping tree of the West Indies, and *Kallstroemia* has some species in Central America (Standley, 1937). Thus, there are 10 genera of xerophytic Zygophyllaceae which do not share the amphitropical distribution attained by *Larrea* (Table 2), including the widely dispersed herbaceous genus, *Peganum*, which has attained an even greater disjunction between the deserts of northern Mexico and northern Africa!

Absence of the genus *Bulnesia* in North and Central America is a particularly difficult anomaly for the continuity theory, because *Bulnesia* has a much wider ecological amplitude than *Larrea*, having two relatively mesophytic species of trees (*B. arborea* Engelm., *B. carrapo* Killip & Dugand.) in humid tropical woodlands north of the equator in Venezuela and Colombia (Porter, 1974). *Bulnesia* parallels *Larrea* in its xeromorphic evolutionary trend with a reduction series from multifoliolate, pinnately compound leaves (as in *B. arborea*) to the bifoliolate leaves of *B. sarmientoi* Lorentz ex Griseb. However, *Bulnesia* also exceeds *Larrea* in the xerophytic direction, inasmuch as *B. retama* occurs in sectors of the South American deserts much too arid for *Larrea divaricata*, or even *L. cuneifolia*. Any continuous route across the tropics, hypothetically traversed by *Larrea*, should have been more readily negotiated by the ecologically more versatile genus *Bulnesia*, with its 8 extant species all endemic to South America. The argument could be extended with the plethora of examples proving a lack

of free exchange between the xerophytic floras of North and South America (Raven, 1963). Also, the insect faunas more or less indigenous to *Larrea* are distinctly different on either side of the amphitropical disjunction (Michener, personal communication; Raven, 1963), a fact strongly suggesting rapid passage through a bottleneck or filter. On the one hand, these biogeographic data defeat the idea of trans-tropic continuity for *Larrea* or most other desert plants in the Americas, but they also point to a South American origin and differentiation for *Larrea*, followed by a relatively recent colonization of the corresponding desert niche in North America by the evolutionarily advanced species, *L. divaricata*.

There remains the major question as to how *Larrea* reached North America. Long-distance transport across the wet tropics seems to be the only feasible possibility (cf. Raven, 1963). Among the available carriers would have been the golden plover (*Pluvialis dominica*), remarkable for its long-distance, nonstop flights during its annual intercontinental migrations between North and South America. Less well known is the similar migration of the upland plover (*Bartramia longicauda*). Unlike most shorebirds (order: Charadriiformes), these two species frequent dry, upland habitats, and winter on the shrub-steppes and grasslands of Argentina. *Pluvialis* winters on the pampas and *Larrea* steppes as far south as Bahía Blanca and inland to the very arid, desert province of Mendoza, while *Bartramia* has similar wintering grounds, but also extends south into the Patagonian *Larrea* country of the Río Negro province (Olrog, 1959; Wetmore et al., 1957: 173). Both species were enormously abundant prior to the onslaught of the market gunners and sportsmen of the late nineteenth century (Hudson, 1918: chap. 21; 1920).

In the northern spring season, when the birds departed from Argentina for their breeding grounds in the Arctic tundra (*Pluvialis*) or the prairies (*Bartramia*) of North America, it was autumn in the southern hemisphere, and the hairy mericarps of *Larrea* were available for dispersal. It has been established by experimental feeding of caged birds that a related charadriid plover, the killdeer (*Charadrius vociferus*), retains some viable seeds in its gizzard for periods as long as 77 to 160 hours, and sometimes up to 340 hours, or about 2 weeks (Proctor, 1968). Since plovers cruise at speeds of about 70 km/hr, with top speed of about 90 km/hr (McLean, 1930), intercontinental transport of ingested seed is indeed possible; a distance of 7,000 km could be traversed in 100 hours of flying time. The very light, densely hairy mericarps of *Larrea* suggest an alternate, ectozoic mode of carriage, possibly cemented to the undertail coverts by the birds' own excrement (the "slovenly plover" mechanism, suggested informally by G. Ledyard Stebbins). On its spring migration the golden plover flies northwestward from Argentina across Bolivia and the Peruvian Andes, and more or less nonstop across Central America, whence it proceeds northward through México, including the arid interior plateau (Wetmore et al., 1957). With millions of birds flying this route for thousands of years, even a seemingly highly improbable event would have been feasible. Thus, diploid South American *Larrea divaricata*, which is at least in part self-compatible (Hunziker et al., 1972; cf. Baker, 1955), could have reached the Chihuahuan Desert of North America by a single, direct dispersal from Argentina. Note, however, the existing

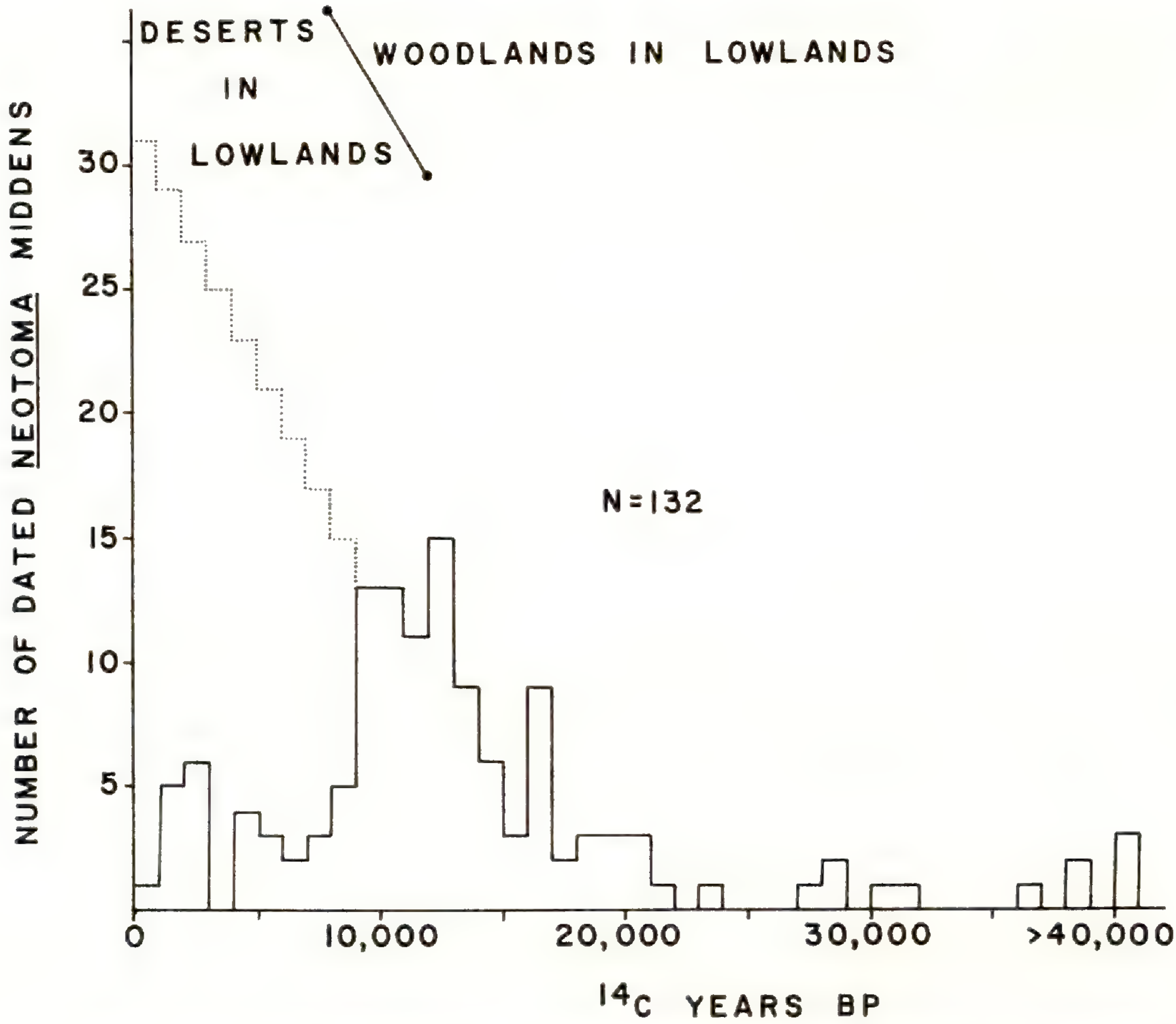

FIGURE 2. Frequency distribution plot of 132 radiocarbon dates obtained on subfossil *Neotoma* middens that have been preserved in dry rock shelters in western North America. The dates are grouped by time intervals of one millenium. The apparent modal peak at 9,000 to 12,000 BP is an artifact of under-representation of the ubiquitously abundant Holocene deposits. An extrapolated projection, based on the late-glacial trend, is added as a dotted line to give a more realistic plot for the Holocene. The vegetational change from pluvial woodland to desert scrub in the lowlands of the Southwest is time transgressive, depending on latitude and elevation of site; cf. Table 1.

way-stations for *Larrea* in northern South America and southern Mexico, mentioned above.

The "way-station" or stepping-stone hypothesis of long-distance migration for amphitropical disjuncts was advocated by Raven (1963), and it appears plausible for some taxa. However, recently obtained data on the chemistry of *Larrea* (Mabry et al., unpublished) argue against the way-station idea for creosote bush. *Larrea tridentata* (North America) shares 85% of 20 flavonoid aglycones with *L. divaricata* from Argentina, but has only 45% of them in common with the northernmost putative "way-station" for *Larrea* in Peru. Unexpectedly, the less distant Peruvian population of *L. divaricata* differs markedly from the Argentinan population, having only 40% of the same set of flavonoids in common. These data support the inference that the Peruvian population of *Larrea* is an older segregate

than the North American vicariad, despite the more dramatic disjunction of the latter. Thus, an *independent* history of isolation is suggested for North American and Peruvian populations of *Larrea*. We infer that *Larrea* colonized North America directly from Argentina, and *not* via Peru, even though the latter station may have been established earlier.

As to the timing of the North American colonization, the paleobotanical evidence is as yet incomplete. Whether *Larrea* arrived in southern Mexico before or during the transition from Pleistocene to Holocene, there is conclusive evidence that the present wide dominance of the *Larrea* zone throughout southwestern North America was not attained before the Holocene (Fig. 2). As discussed above, *Larrea* has not been detected in the full-glacial *Neotoma* record from any part of the Mohave Desert, nor from the Sonoran Desert in southeastern California, northern Baja California, and central Sonora, nor from the Chihuahuan Desert in Texas. During the height of the Wisconsin-age pluvials, any extensive creosote bush deserts must have been displaced far to the south by the great expansion of the woodland zone throughout most of the vast lowlands presently dominated by *Larrea* in southwestern North America. Of course, the current inadequate state of knowledge does not preclude the existence of *Larrea* in one or more North American refugia during the glacials of the Pleistocene, but the available evidence is in agreement with a relatively recent, perhaps late-Wisconsin or early Holocene, age for *Larrea* in North America.

Literature Cited

Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347–348.

———. 1972. Seed weight in relation to environmental conditions in California. Ecology 53: 997–1010.

Barbour, M. G. 1969. Patterns of genetic similarity between *Larrea divaricata* of North and South America. Amer. Midl. Naturalist 81: 54–67.

Bravo, H. 1936. Observaciones florísticas y geobotánicas en el Valle de Actopan. Anales Inst. Biol. Univ. Nac. México 7: 169–233.

———. 1937. Observaciones florísticas y geobotánicas en el valle del Mezquital. Anales Inst. Biol. Univ. Nac. México 8: 3–82.

Britton, N. L. & J. N. Rose. 1920. The Cactaceae. Publ. Carnegie Inst. Wash. 248. (1): 1–236, (2): 1–239, (3): 1–255, (4): 1–318.

Engler, A. 1896. Über die geographische Verbreitung der Zygophyllaceen in Verhältnis zu ihrer systematischen Gliederung. Abh. Königl. Akad. Wiss. Berlin 2: 1–36.

Flint, R. F. 1971. Glacial and Quaternary Geology. Wiley, New York, 892 pp.

Gadgil, M. & O. T. Solbrig. 1972. The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. Amer. Naturalist 106: 14–31.

Goodspeed, T. H. 1954. The Genus Nicotiana. Chronica Botanica, Waltham, Massachusetts. 536 pp.

Hudson, W. H. 1918. Far Away and Long Ago. E. P. Dutton, London.

———. 1920. Birds of La Plata. J. M. Denth & E. P. Dutton, London.

Hunziker, J. H., R. A. Palacios, A. G. de Valesi & L. Poggio. 1972. Species disjunctions in *Larrea*: evidence from morphology, cytogenetics, phenolic compounds, and seed albumins. Ann. Missouri Bot. Gard. 59: 224–233.

Johnston, I. M. 1940. The floristic significance of shrubs common to North and South America. J. Arnold Arbor. 21: 356–363.

Leskinen, P. H. 1970. Late Pleistocene vegetation change in the Christmas Tree Pass area, Newberry Mountains, Nevada. M.S. thesis, Univ. of Arizona, Tucson. 39 pp.

Mabry, T. J., C. Bohnstedt, B. Timmermann & M. Sakakibara. 1977. The natural products chemistry of *Larrea* in the deserts of North and South America. *In* Wauer,

R. H. & D. H. Riskind (editors), Symposium on the Biological Resources of the Chihuahuan Desert Region (in press).

McLEAN, D. D. 1930. The speed of flight in certain birds. Gull 12: 1–2.

MEHRINGER, P. J. & R. HOOKE. 1969. *In* Buckley, J. D. & E. H. Willis, Isotopes' radiocarbon measurements VII. Radiocarbon 11: 53–105.

MORELLO, J. 1958. La provincia fitogeográfica del Monte. Opera Lilloana 2: 1–155.

OLROG, C. C. 1959. Las Aves Argentinas. Inst. Miguel Lillo, Univ. Nacional, Tucuman. 345 pp.

PHILLIPS, A. M. & T. R. VAN DEVENDER. 1974. Pleistocene packrat middens from the lower Grand Canyon of Arizona. J. Arizona Acad. Sci. 9: 117–119.

PORTER, D. M. 1963. The taxonomy and distribution of the Zygophyllaceae of Baja California, Mexico. Contr. Gray Herb. 192: 99–135.

———. 1972. The genera of Zygophyllaceae in the southeastern United States. J. Arnold Arbor. 53: 531–552.

———. 1974. Disjunct distributions in the New World Zygophyllaceae. Taxon 23: 339–346.

PROCTOR, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160: 321–322.

QUINTERO, L. G. 1968. Tipos de vegetación del Valle del Mezquital, Mexico. Ser. Paleoecol., Dept. Prehist., Inst. Nac. Antropol. Hist., México 2: 1–53.

RAVEN, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quart. Rev. Biol. 38: 151–177.

RZEDOWSKI, J. & F. MEDELLÍN LEAL. 1958. El límite sur de distribución geográfica de *Larrea tridentata*. Acta Ci. Potos. 2: 133–147.

SALISBURY, E. J. 1942. The Reproductive Capacity of Plants. G. Bell and Sons, Ltd., London. 244 pp.

SHREVE, F. 1911. The influence of low temperature on the distribution of the giant cactus. Pl. World 14: 136–146.

———. 1942. The desert vegetation of North America. Bot. Rev. (Lancaster) 8: 195–246.

———. 1951. Vegetation of the Sonoran Desert. Publ. Carnegie Inst. Wash. 591: 1–192.

——— & I. L. WIGGINS. 1964. Vegetation and Flora of the Sonoran Desert. Stanford Univ. Press, Stanford. 1, 740 pp.

STANDLEY, P. C. 1937. Flora of Costa Rica. Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1–1616.

TUCKER, J. M. & C. H. MULLER. 1956. The geographic history of *Quercus ajoensis*. Evolution 10: 157–175.

TURNER, B. L. 1972. Chemosystematic data: their use in the study of disjunctions. Ann. Missouri Bot. Gard. 59: 152–164.

VAN DEVENDER, T. R. 1973. Late Pleistocene plants and animals of the Sonoran Desert: a survey of ancient packrat middens in southwestern Arizona. Ph.D. dissertation, Univ. of Arizona, Tucson. 179 pp.

——— & J. E. KING. 1971. Late Pleistocene vegetational records in western Arizona. J. Arizona Acad. Sci. 6: 240–244.

WELLS, P. V. 1959. An ecological investigation of two desert tobaccos. Ecology 40: 626–644.

———. 1965. Vegetation of the Dead Horse Mountains, Brewster County, Texas. Southw. Naturalist 10: 256–260.

———. 1966. Late Pleistocene vegetation and degree of pluvial climatic change in the Chihuahuan Desert. Science 153: 970–975.

———. 1969. Preuves paléontologiques d'une végétation tardi-Pleistocène (datée par le ^{14}C) dans les régions aujourd'hui désertiques d'Amérique du Nord. Rev. Géogr. Phys. Géol. Dynam. 11: 335–340.

———. 1972. Unpublished research proposal submitted to the National Science Foundation. Typescript. 33 pp.

———. 1976. Macrofossil analysis of wood rat (*Neotoma*) middens as a key to the Quaternary vegetational history of arid America. Quaternary Res. 6: 223–248.

———. 1977. Postglacial origin of the Chihuahuan Desert less than 11,500 years ago. *In* Wauer, R. H. & D. H. Riskind (editors), Symposium on the Biological Resources of the Chihuahuan Desert Region (in press).

——— & R. BERGER. 1967. Late Pleistocene history of coniferous woodland in the Mohave Desert. Science 155: 1640–1647.

——— & ———. Unpublished. Radiocarbon dates on fossil material obtained in 1969–1971.
——— & C. D. JORGENSEN. 1964. Pleistocene wood rat middens and climatic change in Mohave Desert: a record of juniper woodlands. Science 143: 1171–1174.
WETMORE, A. et al. 1957. The A.O.U. Check-list of North American Birds. Baltimore. 691 pp.
YANG, T. W. 1967. Ecotypic variation in *Larrea divaricata*. Amer. J. Bot. 54: 1041–1044.
———. 1968. A new chromosome race of *Larrea divaricata* in Arizona. W. Res. Acad. Nat. Hist. Mus. Spec. Publ. 2: 1–4.
———. 1970. Major chromosome races of *Larrea* in North America. J. Arizona Acad. Sci. 6: 41–45.

SEIWA-EN, A NEW JAPANESE GARDEN AT THE MISSOURI BOTANICAL GARDEN

Displayed on the banner of this issue is a very early spring view of a portion of the new Japanese Garden that has been under development since 1974. It has been named *Seiwa-En*, meaning "garden of pure, clear harmony and peace." Designed by Prof. Koichi Kawana, professor of Environmental Design at the University of California, Los Angeles, this beautiful new addition to the Missouri Botanical Garden was formally dedicated 5 May 1977. With a four-acre lake as the focal point, the new garden features, among other things, three islands, two waterfalls, a traditional Japanese teahouse, four bridges of different traditional styles, dry rock gardens, and extensive plantings of trees and shrubs with an emphasis on pines, *Cryptomeria*, *Euonymus*, quince, azaleas, and cherries. Totaling twelve acres, this garden is the largest of its kind in the United States.—*Editor*

CHROMOSOME NUMBERS IN COMPOSITAE. XIII. EUPATORIEAE[1]

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ABSTRACT

New chromosome counts are provided for 234 populations of the tribe Eupatorieae including the first reports for the genera: *Asplundianthus*, *Carminatia*, *Cronquistia*, *Decachaeta*, *Guevaria*, *Heterocondylus*, *Matudina*, *Peteravenia*, *Phalacraea*, *and Sclerolepis*. Chromosome data is summarized on the basis of over 325 of about 2,000 species in the tribe representing 70 of the 160 known genera. Cytology is correlated with recent taxonomic revisions including new generic concepts and reidentification of many vouchers of previous cytological studies. The number $n = 10$ is regarded as basic for the tribe; it is the most common in the tribe and is characteristic of most groups of genera. Important derivatives include specialized members of the *Brickellia* series with $x = 9$ and members of the *Piqueria*, *Stevia*, *Carphochaete*, *Microspermum* series with $x = 11$ and 12. The *Bartlettina* series has a base of $x = 16$ but is closely related to *Hebeclinium* with $x = 10$. Other groups with higher numbers are more distinctive, *Neomirandea* subgenus *Critoniopsis* with $x = 17$, subgenus *Neomirandea* with $x =$ ca. 20 and ca. 25, *Mikania* with $x = 16$–20, *Ageratina* with mostly $x = 17$, *Oxylobus* with $x = 16$. *Hofmeisteria* with $x = 18$–19 is regarded on other bases as one of the most distinctive elements in the tribe. Individual examples of reduction in groups with a base of $x = 10$ are *Adenostemma involucratum* with $n = 5$ and the weedy *Fleischmannia microstemon* with $n = 4$.

The present paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974) and is the first devoted to the tribe Eupatorieae. Included here is a summary of previous studies and combined reports of some of the present authors. An attempt is made to correlate results with the extensive systematic revisions of two of the authors (King, 1967a, 1967b; King & Robinson, 1967, 1969–1975b).

Unless otherwise indicated the chromosome counts have been made from acetocarmine or aceto-orceine squashes of microsporocytes in meiosis. Voucher specimens are available for all counts. Vouchers for the King collections are in the U.S. National Herbarium (US) and a nearly complete set is at the Missouri Botanical Garden (MO). Vouchers for other collections are deposited in the Dudley Herbarium (DS), Stanford University, unless otherwise indicated. In Table 1 those collection numbers preceded by *B* are by Breedlove, by *K* are by King, and by *R* are by Raven.

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Of the approximately 2,000 species of the Eupatorieae, chromosome numbers are known for 327 species. These include members of 70 of the 160 known genera. Nine genera, *Asplundianthus*, *Carminatia*, *Cronquistia*, *Decachaeta*, *Guevaria*, *Heterocondylus*, *Matudina*, *Peteravenia*, *Phalacraea*, and *Sclerolepis*, are newly reported in this paper. The 56 species reported here for the first time are marked by an asterisk in Table 1.

Evaluation of previous reports has required reorganization of data into new tribal and generic concepts based largely on details of floral anatomy. The tribe Eupatorieae is interpreted here to include *Isocarpha* and *Lepidesmia* which are sometimes placed in the Heliantheae (King & Robinson, 1970f), and *Microspermum* and *Iltisia* which are sometimes placed in the Helenieae (Rzedowski, 1970). Excluded are *Adenostyles*, now placed in the Senecioneae (Toman et al., 1968) and *Dyscritothamnus* which is a member of the Heliantheae.

Revisions at the generic level have provided the most significant basis for interpreting cytological data. The most striking example is the dissection of the older concept of *Eupatorium*, a genus which had over 900 species. These species had a meaningless series of chromosome numbers, including $n = 4$, 8, 10, 11, 12, 15, 17, 18, 20, 25 and multiples. One other species falling within the old concept had been counted at $n = 9$, but was removed to *Brickellia* on the basis of this chromosome number (Harcombe & Beaman, 1967). Other generic concepts have been altered to a lesser extent. The chromosome numbers credited to *Alomia* belong to species that have been transferred to *Ageratum*. In *Piqueria*, chromosome counts of $n = 10$, 12, 24, and 25 have been reported, but the determination of $n = 10$ is from a South American species now placed in the genus *Ophryosporus*.

Many previous reports have been based on misidentified material and some of these represent generic differences. Reports for what is generally called *Eupatorium ballotifolium* H.B.K. (Coleman, 1968, 1970) are not of that species but of *Conocliniopsis prasiifolia* (DC.) K. & R. The true *E. ballotifolium* is a *Lourteigia* and has been reported as *Eupatorium* aff. *pycnocephaloides* (Powell & King, 1969). The latter species is a *Fleischmannia* and is reported for the first time in this paper. Chromosome counts reported for *Trichogonia gardneri* Gray should be treated under the name *Trichogoniopsis adenantha* (DC.) K. & R. Asa Gray had erroneously considered the two species as distinct. Material in most herbaria under the name *E. adenanthum* actually belongs to the distinct genus *Macropodina*. A report of $n = 10$ has been credited to *Eupatorium* cf. *ligustrinum* (Turner et al., 1961) which is a member of the genus *Ageratina*, a genus which has a basic chromosome number of $x = 17$. The voucher has been seen and proves to be *Koanophyllon albicaule* (Sch.-Bip. ex Klatt) K. & R. Some additional corrections of identification within genera are mentioned below, with notable examples in *Adenostemma* and *Fleischmannia*.

General Considerations

Gaiser (1954) observed that chromosome numbers lower than $n = 9$ did not occur in the *Eupatorieae*. Since that time the gametic chromosome number $n = 4$ has been discovered in two species of *Fleischmannia*, a number of $n = 5$ has

TABLE 1. Chromosome counts, localities and vouchers for species of Eupatorieae.

Species	*n*	Locality and collection number
Adenostemma platyphyllum Cass.	10	ECUADOR. EL ORO: ca. 30 kms NE of Machala, *K6934*.
Adenostemma platyphyllum	10	ECUADOR. CHIMBORAZO: 35 kms NE of El Triunfo, *K6955*.
Adenostemma platyphyllum	10	ECUADOR. CAÑAR: 71 kms ESE of Guayaquil, *K6869*.
Ageratina altissima (L.) K. & R.	ca. 17	UNITED STATES. NORTH CAROLINA: Haywood Co., *R20479*.
Ageratina altissima	ca. 17	UNITED STATES. INDIANA: Monroe Co., *R20499*.
Ageratina anisochroma (Klatt) K. & R.	ca. 17	COSTA RICA. SAN JOSÉ: ca. 17 kms NW of Empalme, *K6411*.
Ageratina anisochroma	17	COSTA RICA. ALAJUELA: Volcán Poás, *K6428*.
Ageratina anisochroma	17	COSTA RICA. SAN JOSÉ: La Palma, *K6740*.
Ageratina anisochroma	ca. 17	COSTA RICA. SAN JOSÉ: La Palma, *K6741*.
Ageratina anisochroma	17	COSTA RICA. CARTAGO: ca. 9 kms NE of San Rafael de Irazú, *K6836*.
Ageratina aschenborniana (Schauer) K. & R.	17	MEXICO. CHIAPAS: Mun. Puebla Nuevo Solistahuacán, *R19926*.
Ageratina aschenborniana	ca. 20	COSTA RICA. SAN JOSÉ: ca. 25 kms S of Cartago, *K6755*.
Ageratina aschenborniana	ca. 17	COSTA RICA. CARTAGO: El Muñeco, *K6770*.
Ageratina aschenborniana	17	COSTA RICA. SAN JOSÉ: ca. 3 kms N of El Copey, *K6789*.
Ageratina aschenborniana	17	COSTA RICA. CARTAGO: 2 kms NE of Santa Rosa, *K6814*.
Ageratina aschenborniana	ca. 17	COSTA RICA. CARTAGO: ca. 3 kms S of Pacayas, *K6830*.
Ageratina aschenborniana	ca. 84_{I} (2 cells ca. $160–166_{I}$)	GUATEMALA. SAN MARCOS: 6 kms NW of Palestina, *K7035*.
Ageratina aschenborniana	ca. 10	GUATEMALA. TOTONICAPÁN: 49 kms ESE of San Cristóbal Totonicapán, *K7061*.
**Ageratina azangaroensis* (Sch.-Bip. ex Wedd.) K. & R.	17	ECUADOR. COTOPAXI: ca. 27 kms S of Aloag, *K6519*.
Ageratina azangaroensis	17_{II} + 1 frag.	ECUADOR. TUNGURAHUA: 1 km SE of Ambato, *K6532*.
Ageratina azangaroensis	17	ECUADOR. CHIMBORAZO: ca. 6 kms S of Mocha, *K6580*.
Ageratina azangaroensis	17	ECUADOR. BOLÍVAR: ca. 22 kms NE of Guaranda, *K6593*.
Ageratina azangaroensis	17_{II} + 1 frag.	ECUADOR. AZUAY: ca. 22 kms W of Cuenca, *K6667*.
Ageratina azangaroensis	17_{II} + 21 or round frag.	ECUADOR. CHIMBORAZO: 45 kms SW of Riobamba, *K6974*.
**Ageratina barbensis* K. & R.	17	COSTA RICA. HEREDIA: ca. 22 kms N of Barba, *K6409*.
**Ageratina bellidifolia* (Benth.) K. & R.	68–69	MEXICO. CHIAPAS: Mun. Chamula, *B8005*.
**Ageratina chiapensis* (B. L. Rob.) K. & R.	ca. 16	MEXICO. CHIAPAS: Mun. Chamula, *B6670*.
Ageratina chiapensis	17	MEXICO. CHIAPAS: San Cristóbal las Casas, *B9054*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
**Ageratina conspicua* (Kunth & Bouche) K. & R.	ca. 25	MEXICO. CHIAPAS: Mun. Chamula, *B9800*.
**Ageratina costaricensis* K. & R.	$70–100_I$	COSTA RICA. CARTAGO: ca. 1 km NE of San Rafael de Irazú, *K6816*.
**Ageratina exerto-venosa* (Klatt) K. & R.	ca. 42	ECUADOR. AZUAY: ca. 17 kms E of Gualacéo, *K6632*.
Ageratina exerto-venosa	ca. 40 + B chromosomes	ECUADOR. AZUAY: 32 kms S of Cumbe, *K6899*.
Ageratina exerto-venosa	ca. 40 + B chromosomes	ECUADOR. LOJA: 2 kms E of Loja, *K6914*.
Ageratina exerto-venosa	ca. 40	ECUADOR. LOJA: 2 kms E of Loja, *K6915*.
Ageratina cf. *glechonophylla* (Less.) K. & R.	17_{II} + 2 frags.	ECUADOR. BOLIVAR: ca. 28 kms SW of Ambato, *K6587*.
**Ageratina ixioclada* (Benth. ex Oerst.) K. & R.	17	COSTA RICA. CARTAGO: 3 kms NE of San Rafael de Irazú, *K6818*.
**Ageratina ligustrina* (DC.) K. & R.	17	MEXICO. CHIAPAS: Mun. Tenejapa, *B6805*.
Ageratina ligustrina	ca. 50	MEXICO. CHIAPAS: Mun. Chamula, *B7797*.
Ageratina ligustrina	55	MEXICO. HIDALGO: Zimapán (progeny) *R13777*, *R13830*.
**Ageratina mairetiana* (DC.) K. & R.	17	MEXICO. CHIAPAS: Mun. Zinacantán, *B9505*.
Ageratina mairetiana	17	MEXICO. OAXACA: Monte Alban, *K6462*.
Ageratina petiolaris (DC.) K. & R.	17	MEXICO. CHIAPAS: San Cristóbal las Casas, *R20062*.
**Ageratina pichinchensis* (H.B.K.) K. & R.	30–34	ECUADOR. CAÑAR: ca. 14 kms NW of Azogues, *K6616*.
Ageratina pichinchensis	33 ± 2	ECUADOR. AZUAY: ca. 14 kms W of Cuenca, *K6656*.
Ageratina pichinchensis	ca. 30	ECUADOR. CHIMBORAZO: 20 kms SW of Riobamba, *K6964*.
Ageratina aff. *pringlei* (B. L. Rob. & Greenm.) K. & R.	17	MEXICO. CHIAPAS: Mun. Zinacantán, *B7987*.
**Ageratina pseudochilca* (Benth.) K. & R.	ca. 42	ECUADOR. AZUAY: 17 kms S of Cumbe, *K6891*.
**Ageratina subcordata* (Benth. ex Oerst.) K. & R.	17	COSTA RICA. SAN JOSÉ: ca. 18 kms SW of Empalme, *K6412*.
Ageratina sp.	17	MEXICO. CHIAPAS: Mun. Chamula, *B6725*.
Ageratina sp.	17	MEXICO. CHIAPAS: Mun. La Trinitaria, *B9741*.
Ageratum houstonianum Mill.	20	ECUADOR. TUNGURAHUA: ca. 7 kms E of Baños, *K6543*.
Ageratum houstonianum	10	MEXICO. CHIAPAS: Mun. Las Margaritas, *B9135*.
Ageratum nelsonii (B. L. Rob.) M. F. Johnson	ca. 10	MEXICO. CHIAPAS: Tapanatepec, *B13722*.
Ageratum rugosum Coult.	10	MEXICO. CHIAPAS: Tuxtla Gutiérrez, *B13892*.
**Aristeguietia buddleaefolia* (Benth.) K. & R.	10	ECUADOR. AZUAY: ca. 12 kms N of Gualacéo, *K6626*.
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: ca. 10 kms SE of Gualacéo, *K6628*.
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: ca. 16 kms N of Sigsig, *K6645*.
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: ca. 7 kms S of Paute, *K6692*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Aristeguietia buddleaefolia	10	ECUADOR. AZUAY: 6 kms SE of Cumbe, *K6692*.
Aristeguietia buddleaefolia	10 or 11	ECUADOR. AZUAY: 5–6 kms NE of Cuenca, *K6873*.
Aristeguietia buddleaefolia	ca. 10	ECUADOR. AZUAY: 10 kms SE of Cumbe, *K6887*.
Aristeguietia buddleaefolia	ca. 10	ECUADOR. AZUAY: 12 kms SE of Cumbe, *K6889*.
**Aristeguietia dielsii* (B. L. Rob.) K. & R.	10	ECUADOR. TUNGURAHUA: 48 kms NE of Guranda, *K6984*.
**Aristeguietia glutinosa* (H.B.K.) K. & R.	10	ECUADOR. CHIMBORAZO: ca. 16 kms W of San Juan, *K6603*.
**Asplundianthus pseudoglomeratus* (Hieron.) K. & R.	ca. 10	ECUADOR. PICHINCHA: ca. 3 kms SW of Chillogallo, *K6510*.
Asplundianthus pseudoglomeratus	10	ECUADOR. PICHINCHA: ca. 10 kms W of Quito, *K6732*.
Austroeupatorium inulaefolium (H.B.K.) K. & R.	10	ECUADOR. TUNGURAHUA: ca. 11 kms E of Baños, *K6547*.
Austroeupatorium inulaefolium	10	ECUADOR. LOJA: 4 kms E of Loja, *K6917*.
**Ayapana ecuadorensis* K. & R.	10	ECUADOR. CAÑAR: 24 kms ESE of El Triunfo, *K7000*.
Ayapana ecuadorensis	10	ECUADOR. CAÑAR: 77 kms ESE of Guayaquil, *K6872*.
**Bartlettina breedlovei* K. & R.	16	GUATEMALA. Mun. San Mateo Ixtatán, *B8717*.
Bartlettina breedlovei	16	MEXICO. CHIAPAS: San Cristóbal las Casas, *B9075*.
**Bartlettina guatemalensis* K. & R.	16	GUATEMALA. Mun. San Mateo Ixtatán, *B8718*.
Bartlettina sordida (Less.) K. & R.	16	MEXICO. CHIAPAS: Mun. Tenejapa, *B9408*.
**Bartlettina tuerckheimii* (Klatt) K. & R.	16	MEXICO. CHIAPAS: Mun. Jitotal, *R19794*.
Brickellia adenocarpa B. L. Rob. var. *glandulipes* B. L. Rob.	ca. 9	MEXICO. CHIAPAS: Mun. Teopisca, *R20067*.
**Brickellia arguta* B. L. Rob.	9	UNITED STATES. NEW MEXICO: Nye Co., *R18931*.
Brickellia argyrolepis B. L. Rob.	9	COSTA RICA. ALAJUELA: 2 kms SW of Zarcero, *K6431*.
**Brickellia atractyloides* A. Gray	9	UNITED STATES. ARIZONA: Mohave Co., *R17366*.
Brickellia californica T. & G.	9	UNITED STATES. CALIFORNIA: Los Angeles Co., *R11350*.
**Brickellia guatemalensis* B. L. Rob.	9	MEXICO. CHIAPAS: Mun. Chamula, *B8014*.
Brickellia guatemalensis	9	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B8081*.
Brickellia guatemalensis	9	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *R20063*.
Brickellia incana A. Gray	$2n = 27$	UNITED STATES. CALIFORNIA: San Bernardino Co., *R15494*.
**Brickellia leptophylla* (Scheele) Shinners	9	MEXICO. DURANGO: Ciudad Durango, *B15507*.
Brickellia schaffneri (A. Gray) Shinners	9	MEXICO. JALISCO: San Juan del Río, *B15460*.
Brickellia veronicifolia (H.B.K.) A. Gray	9	MEXICO. PUEBLA: Tehuacán, *B14191*.
**Carminatia tenuifolia* DC.	10	MEXICO. CHIAPAS: Tuxtla Gutiérrez, *B13346*.
**Chromolaena collina* (DC.) K. & R.	10	MEXICO. CHIAPAS: Tapanatepec, *B8837*.
Chromolaena laevigata (Lam.) K. & R.	ca. 20	ECUADOR. LOJA: ca. 27 kms W of Chinchas, *K6929*.
Chromolaena laevigata	ca. 20	ECUADOR. TUNGURAHUA: E of Baños, *K6987*.

TABLE 1. (Continued).

Species	n	Locality and collection number
Chromolaena odorata (L.) K. & R.	30	MEXICO. SINALOA: Concordia (progeny), *B1596*.
Chromolaena odorata	ca. 31 + 41	MEXICO. CHIAPAS: Mun. Bochil, *B8837*.
Chromolaena odorata	60_I	MEXICO. CHIAPAS: Mun. Tenejapa, *B9430*.
**Chromolaena opadoclina* (Blake) K. & R.	10	MEXICO. CHIAPAS: Mun. Jitotal, *R19935*.
Chromolaena sagittata (A. Gray) K. & R.	20	MEXICO. SINALOA: Río de Presidoa (progeny), *B1580*.
Condylidium iresinoides (H.B.K.) K. & R.	10	ECUADOR. GUAYAS: 33 kms NE of El Triunfo, *K6951*.
Conoclinium coelestinum (L.) DC.	10	UNITED STATES. LOUISIANA: Bossier Parish, *R20391*.
**Critonia hospitalis* (B. L. Rob.) K. & R.	ca. 10	MEXICO. CHIAPAS: Tuxtla Gutiérrez, *B13869*.
Critonia morifolia (Miller) K. & R.	10	GUATEMALA. SACATEPEQUEZ: Ciudad Vieja, *K7077*.
Critonia morifolia	10	GUATEMALA. GUATEMALA: 20 kms E Villa Canales, *K7083*.
**Critonia sexangularis* (Klatt) K. & R.	10	MEXICO. CHIAPAS: Mun. Pueblo Nuevo Solistahuacán, *R20010*.
**Cronquistia pringlei* (S. Watson) R. M. King	12	MEXICO. DURANGO: Ciudad Durango, *B15512*.
**Decachaeta incompta* (DC.) K. & R.	16	MEXICO. CHIAPAS: Ixtapa, *B14062*.
Eupatoriadelphus maculatus (L.) K. & R.	10	UNITED STATES. NEW HAMPSHIRE: Chesire Co., *Gregory 495*.
Eupatoriadelphus maculatus	10	UNITED STATES. MICHIGAN: St. Joseph Co., *R20512*.
Eupatoriadelphus purpureus (L.) K. & R.	10	UNITED STATES. TENNESSEE: Van Buren Co., *R20443*.
Eupatoriadelphus purpureus	10	UNITED STATES. NORTH CAROLINA: McDowell Co., *R20474*.
Eupatorium hyssopifolium L. var. *hyssopifolium*	20	UNITED STATES. TENNESSEE: Monroe Co., *R20486*.
Eupatorium perfoliatum L.	10	UNITED STATES. MISSOURI: Wayne Co., *R20486*.
Eupatorium perfoliatum	10	UNITED STATES. TENNESSEE: Loudon Co., *R20491*.
Eupatorium rotundifolium L. var. *ovatum* (Bigel.) Torrey	20	UNITED STATES. TEXAS: Hardin Co., *R19433*.
Eupatorium rotundifolium var. *ovatum*	$2n = 39$–40	UNITED STATES. NORTH CAROLINA: McDowell Co., *R20484*.
Eupatorium serotinum Michx.	10	UNITED STATES. TENNESSEE: Monroe Co., *R20484*.
Eupatorium serotinum	10	UNITED STATES. INDIANA: Monroe Co., *R20500*.
Eupatorium serotinum	10	UNITED STATES. MISSOURI: Francois Co., *R20532*.
Eupatorium serotinum	10	UNITED STATES. ARKANSAS: Saline Co., *R20564*.
**Fleischmannia capillipes* (Benth. ex Oerst.) K. & R.	ca. 10	MEXICO. CHIAPAS: Tapanatepec, *B13713*.
**Fleischmannia imitans* (B. L. Rob.) K. & R.	29	MEXICO. CHIAPAS: Mun. Chiapa del Corzo, *R19773*.
**Fleischmannia pastazae* (B. L. Rob.) K. & R.	20	ECUADOR. TUNGURAHUA: ca. 21 kms E of Baños, *K6553*.
Fleischmannia pastazae	20	ECUADOR. TUNGURAHUA: ca. 2 kms E of Río Negro, *K6556*.
**Fleischmannia plectranthifolia* (Benth. ex Oerst.) K. & R.	10	COSTA RICA. HEREDIA: ca. 15 kms N of Barba, *K6410*.
Fleischmannia pratensis (Klatt) K. & R.	20	MEXICO. CHIAPAS: Mun. Las Margaritas, *B9134*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Fleischmannia pratensis	20	MEXICO. CHIAPAS: Ocozocuatla de Espinosa, *B10326*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: 11 kms E of Pacayas, *K6540*.
Fleischmannia pratensis	ca. 20	ECUADOR. TUNGURAHUA: ca. 7 kms E of Baños, *K6540*.
Fleischmannia pratensis	20	COSTA RICA. SAN JOSÉ: La Palma, *K6737*.
Fleischmannia pratensis	ca. 20	COSTA RICA. SAN JOSÉ: ca. 16 kms W of Santa Ana, *K6747*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: El Muñeco, *K6767*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: El Muñeco, *K6768*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: Navarro, *K6772*.
Fleischmannia pratensis	ca. 20	COSTA RICA. CARTAGO: 2 kms SW of Tapantí, *K6775*.
Fleischmannia pratensis	20	COSTA RICA. SAN JOSÉ: ca. 8 kms N of Nubes, *K6780*.
Fleischmannia pratensis	20	COSTA RICA. HEREDIA: ca. 2 kms SW of Alto Gallito, *K6802*.
Fleischmannia pratensis	20	COSTA RICA. HEREDIA: ca. 9 kms N of Barba, *K6809*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: 1 km NE of Santa Rosa, *K6813*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: ca. 6 kms NE of San Rafael de Irazú, *K6827*.
Fleischmannia pratensis	20	COSTA RICA. CARTAGO: ca. 8 kms W of Tucurrique, *K6845*.
Fleischmannia pycnocephala (Less.) K. & R.	30	MEXICO. CHIAPAS: Mun. La Trinitaria, *B8389*.
Fleischmannia pycnocephala	30	GUATEMALA. Mun. San Mateo Ixtatán, *B8674*.
Fleischmannia aff. *pycnocephala*	20	MEXICO. CHIAPAS: Teopisca, *B13079*.
Fleischmannia pycnocephala	20	MEXICO. OAXACA: El Tejocote, *K6451*.
Fleischmannia pycnocephala	20	MEXICO. VERACRUZ: 7 kms SW of Coscomatepec, *K6488*.
Fleischmannia pycnocephala	ca. 40	GUATEMALA. ALTA VERAPAZ: 5 kms NE of San Pedro Carchá, *K7125*.
Fleischmannia pycnocephala	42–44 + 2–4$_1$	GUATEMALA. BAJA VERAPAZ: ca. 53 kms SE Cobán, *K7128*.
**Fleischmannia pycnocephaloides* (B. L. Rob.) K. & R.	30	GUATEMALA. HUEHUETENANGO: San Juan Ixcoy, *B8468*.
**Fleischmannia seleriana* (B. L. Rob.) K. & R.	10	MEXICO. VERACRUZ: 3 kms W of Ciudad Mendoza, *K6485*.
Fleischmannia sp.	12 + 1–3$_1$ (rarely 13 looking or 11 + 3$_1$)	GUATEMALA. SACATEPEQUEZ: Ciudad Vieja, *K7078*.
Fleischmannia sp.	10	GUATEMALA. ALTA VERAPAZ: San Cristóbal Verapaz, *K7110*.
**Guevaria alvaroi* K. & R.	10	ECUADOR. AZUAY: ca. 11 kms NE of Girón, *K6673*.
**Guevaria sodiroi* (Hieron. ex Sod.) K. & R.	10	ECUADOR. CAÑAR: ca. 13 kms NW of Azogues, *K6615*.
Guevaria sodiroi	10	ECUADOR. CAÑAR: ca. 14 kms NW of Azogues, *K6617*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 14 kms W of Cuenca, *K6655*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 19 kms W of Cuenca, *K6664*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 6 kms SE of Cumbe, *K6698*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 7 kms SE of Cumbe, *K6706*.
Guevaria sodiroi	10	ECUADOR. AZUAY: ca. 13 kms S of Cumbe, *K6714*.
Guevaria sodiroi	10	ECUADOR. CAÑAR: 20 kms NW of Azogues, *K6882*.
Guevaria sodiroi	10	ECUADOR. AZUAY: 39 kms S of Cumbe, *K6904*.
**Hebeclinium bullatissimum* (B. L. Rob.) K. & R.	10	ECUADOR. TUNGURAHUA: ca. 2 kms E of Río Negro, *K6557*.
Hebeclinium bullatissimum	10	ECUADOR. TUNGURAHUA: ca. 26 kms N of Puyo, *K6571*.
Hebeclinium macrophyllum (L.) DC.	10	MEXICO. CHIAPAS: Ocozocuatla, *B13580*.
Hebeclinium macrophyllum	10	ECUADOR. CAÑAR: 71 kms ESE of Guayaquil, *K6868*.
**Heterocondylus vitalbae* (DC.) K. & R.	ca. 20	COSTA RICA. CARTAGO: Navarro, *K6774*.
Hofmeisteria fasciculata (Benth.) Walp.	18	MEXICO. BAJA CALIFORNIA: Bahía de la Concepción, *Wiggins 19000*.
Isocarpha atripicifolia (L.) R. Brown	10	GUATEMALA. ZACAPA: ca. 4 kms NNW of Zacapa, *K7376*.
Isocarpha oppositifolia (L.) R. Brown	10	MEXICO. YUCATAN: Chichén Itzá, *K6859*.
**Koanophyllon hylonomum* (B. L. Rob.) K. & R.	10	COSTA RICA. ALAJUELA: 12 kms N of Quesada, *K6432*.
**Koanophyllon ravenii* K. & R.	ca. 10	MEXICO. CHIAPAS: Chiapa del Corzo, *B13472*.
Malperia tenuis S. Watson	10	MEXICO. BAJA CALIFORNIA: 2.7 mi W of San Felipe, *R14764* (DS).
**Matudina corvii* (McVaugh) K. & R.	16	MEXICO. CHIAPAS: Chiapa de Corzo, *B13473*.
Mikania micrantha H.B.K.	17	ECUADOR. TUNGURAHUA: ca. 11 kms E of Baños, *K6544*.
Mikania micrantha	ca. 19	ECUADOR. CAÑAR: 71 kms ESE of Guayaquil, *K6870*.
Mikania micrantha	19	ECUADOR. CAÑAR: 23 kms ESE of El Triunfo, *K6999*.
**Mikania scandens* (L.) Willd.	ca. 19	UNITED STATES. DELAWARE: Sussex Co., *K6847, K6848*.
**Mikania vitifolia* DC.	ca. 20	ECUADOR. CAÑAR: 26 kms ESE of El Triunfo, *K7001*.
**Neomirandea allenii* K. & R.	17–20	PANAMA. COCLÉ: La Mesa, *Croat 37430*.
Neomirandea angularis (B. L. Rob.) K. & R.	ca. 24	COSTA RICA. CARTAGO: 20 kms SE of Orosi, *K6419*.
Neomirandea angularis	ca. 20	COSTA RICA. SAN JOSÉ: La Palma, *K6422*.
**Neomirandea biflora* K. & R.	ca. 25	COSTA RICA. CARTAGO: ca. 9 kms NE of San Rafael de Irazú, *K6835*.
**Neomirandea burgeri* K. & R.	20	COSTA RICA. SAN JOSÉ: Cerro de la Muerte, *K6413*.
Neomirandea costaricensis K. & R.	17	COSTA RICA. SAN JOSÉ: ca. 17 kms SE of Empalme, *K6760*.
Neomirandea costaricensis	ca. 17	COSTA RICA. SAN JOSÉ: ca. 8 km SE of Empalme, *K6764*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Neomirandea costaricensis	17	COSTA RICA. SAN JOSÉ: ca. 9 kms SE of Cañon, *K6791*.
Neomirandea costaricensis	17_{II} + 1 B chromosome	COSTA RICA. HEREDIA: ca. 10 kms N of San Rafael, *K6796*.
Neomirandea costaricensis	17	COSTA RICA. HEREDIA: ca. 2 kms SW of Alto Gallito, *K6801*, *K6804*.
**Neomirandea eximia* (B. L. Rob.) K. & R.	17	COSTA RICA. SAN JOSÉ: La Palma, *K6738*, *K6739*, *K6742*.
Neomirandea eximia	ca. 17	COSTA RICA. SAN JOSÉ: ca. 25 kms S of Cartago, *K6756*.
Neomirandea eximia	17 + 4– 5 supernumerary chromosomes	COSTA RICA. HEREDIA: ca. 2 kms SW of Alto Gallito *K6803*.
**Oxylobus oaxacanus* Blake	16	MEXICO. CHIAPAS: San Cristóbal las Casas, *B9587*.
**Peteravenia phoenicolepis* (B. L. Rob.) K. & R.	10	MEXICO. CHIAPAS: Mun. Chamula, *B7315*.
Peteravenia phoenicolepis	10	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B8289*.
Peteravenia phoenicolepis	ca. 17	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B14148*.
**Phalacraea ecuadorensis* K. & R.	20	ECUADOR. AZUAY: ca. 14 kms W of Cuenca, *K6653*.
Piqueria trinervia Cav.	11	MEXICO. CHIAPAS: Mun. La Trinitaria, *B8390*.
Piqueria trinervia	11	MEXICO. CHIAPAS: Teopisca, *B13086*.
Piqueria trinervia	ca. 24	COSTA RICA. CARTAGO: Volcán Irazú, *K6438*.
Piqueria trinervia	ca. 22 + 1–2 frags.	COSTA RICA. CARTAGO: ca. 3 kms NE of Cot, *K6812*.
Pleurocoronis pluriseta (A. Gray) K. & R.	9	UNITED STATES. CALIFORNIA: Riverside Co., *R11465*.
Pleurocoronis pluriseta	9	MEXICO. SONORA: Punta Peñasco, *R11665*.
Polyanthina nemorosa (Klatt) K. & R.	10 (2 larger bivalents)	ECUADOR. TUNGURAHUA: ca. 2 kms E of Río Negro, *K6559*.
**Sclerolepis uniflora* (T. Walter) Porter	15	UNITED STATES. NEW JERSEY: Cape May Co., *K7150* (part).
Sclerolepis uniflora	ca. 30	UNITED STATES. NEW JERSEY: Cape May Co., *K7150* (part).
Stevia berlandieri A. Gray	12	MEXICO. DURANGO: El Palmito, *B14187*.
Stevia elatior H.B.K.	ca. 23	MEXICO. CHIAPAS: Mun. Chamula, *B7067*.
Stevia elatior	11	MEXICO. OAXACA: El Tejocote, *K6459*.
Stevia elatior	11	ECUADOR. LOJA: 2 kms E of Loja, *K6909*.
Stevia elatior	ca. 33_{I}	GUATEMALA. HUEHUETENANGO: 53 kms N of Quezaltenango, *K7048*.
Stevia elatior	ca. 33_{I}	GUATEMALA. TOTONICAPÁN: 31 kms S of Huehuetenango, *K7050*.
Stevia elatior	ca. 33_{I}	GUATEMALA. TOTONICAPÁN: 10 kms E of Totonicapán, *K7068*.

TABLE 1. (Continued).

Species	*n*	Locality and collection number
Stevia lucida Lag.	12	MEXICO. CHIAPAS: San Cristóbal las Casas, *B7120.*
Stevia ovata Willd.	34_I	MEXICO. CHIAPAS: Teopisca, *B13070.*
Stevia ovata	ca. 60_I	MEXICO. CHIAPAS: Mun. Chamula, *B13737.*
Stevia ovata	$32–34_I$	MEXICO. CHIAPAS: Ixtapa, *B14061.*
Stevia ovata	36_I	MEXICO. CHIAPAS: San Cristóbal las Casas, *B14153.*
Stevia ovata	36_I	GUATEMALA. ALTA VERAPAZ: 4 kms W of San Cristóbal Verapaz, *K7111.*
Stevia polycephala Bertol.	12	MEXICO. CHIAPAS: Mun. Zinacantán, *B7995.*
Stevia polycephala	12	MEXICO. CHIAPAS: Mun. San Cristóbal las Casas, *B8302.*
Stevia polycephala	12	GUATEMALA. HUEHUETENANGO: Mun. San Juan Ixcoy, *B8495.*
Stevia polycephala	12	GUATEMALA. SAN MARCOS: 5 kms SE of Palestina, *K7031.*
Stevia polycephala	12	GUATEMALA. SAN MARCOS: 20 kms NE of San Marcos, *K7040.*
Stevia polycephala	12	GUATEMALA. TOTONICAPÁN: 12 kms SE of San Cristóbal Totonicapán, *K7054.*
Stevia serrata Cav.	ca. 27	MEXICO. CHIAPAS: Mun. Chamula, *B6650.*
Stevia serrata	ca. 33_I	GUATEMALA. TOTONICAPÁN: 21 kms NE of Quezaltenango, *K7042.*
Stevia serrata	ca. 54_I	GUATEMALA. TOTONICAPÁN: 24 kms NE of Quezaltenango, *K7043.*
Stevia subpubescens Lag.	12	MEXICO. SINALOA: El Palmito, *B14184.*
Stevia subpubescens	ca. 12	MEXICO. MORELOS: Tres Cumbres, *B14229.*
**Stevia tephrophylla* Blake	12	MEXICO. CHIAPAS: Ocozocuatla, *B13643.*
Stevia tephrophylla	ca. 12	MEXICO. CHIAPAS: Ocozocuatla, *B10346.*
Stevia trifida Lag.	11	MEXICO. SINALOA: Concordia, *B1647.*

* First chromosome number report for this species.

been reported for one species of *Adenostemma*, and $n = 8$ has been suggested, probably erroneously, for species of *Isocarpha* and *Ayapana*. It is probable that no other tribe in the family, except the Cynareae and Mutisieae, has as few species with low chromosome numbers.

Differences in chromosome size and shape have been mentioned in the studies of Grant (1953) and Gaiser (1953, 1954). While dealing with *Eupatorium* s. lat. in eastern North America, Grant reported two size ranges of chromosomes. For species now treated as *Eupatorium* s. str. and *Eupatoriadelphus*, with $n = 10$, the size ranged from 2.5–6.5 μm in length. For the group now recognized as *Ageratina*, with $n = 17$, the size ranged between 1.5–3.0 μm. One species now recognized as a *Conoclinium* has $n = 10$, as in the former group, but the chromosomes fall within the size range of the latter group. Grant treated these three groups as cytologically distinct.

Gaiser (1954) compared the taxa then placed in the subtribe Kuhniinae. This subtribe has since been shown to be artificial, so that Gaiser's comparison was between three groups that we do not now consider closely related. *Carphochaete* was distinguished as a small shrub without basal rosettes having a squamiform pappus and a gametic chromosome number of $n = 11$. The genus had the highest chromosome number and greatest content of chromatin per complement; it also had 3 pairs of isobrachial short chromosomes. The genera *Garberia*, *Carphephorus*, *Liatris*, and *Trilisa* (including *Latrisa*) were distinguished by alternate leaves forming basal rosettes in younger plants, a plumose or capillary pappus, and a gametic chromosome number of $n = 10$. *Garberia* was distinct among these in being a shrub and in having one of the two short pairs of chromosomes heterobrachial. The third group of genera, including *Brickellia*, *Kuhnia* and *Barroetia*, had leaves alternate to opposite, plants shrubby to annual without basal rosettes, pappus capillary to plumose, and a gametic chromosome number of $n = 9$. *Barroetia* and *Kuhnia* both had only medium and short chromosomes. *Brickellia* (Gaiser, 1953) had chromosomes of some species as in *Kuhnia* and *Barroetia*, but in most species the complements included longer chromosomes.

Gaiser (1953, 1954) noted the variation in karyotype in the *Brickellia* series and correlated this with variation in habit of the plants. Karyotypes including some long chromosomes were characteristic of shrubby plants. Karyotypes with only medium or short chromosomes occurred in more herbaceous plants. An apparent trend toward reduced DNA content in weedy species (Bennett, 1972) is also illustrated in the tribe in the genus *Fleischmannia*, in which a weedy annual species has a gametic chromosome number of $n = 4$, with most other species being perennial and having $n = 10$ and multiples of 10.

Pollen and Cell Size Correlation

Gaiser (1950b) made observations on morphological characters in relation to polyploidy in *Liatris* series *Punctatae*. Overall size showed no reliable correlation with chromosome number though corollas, styles, pappus, and inner phyllaries tended to be slightly longer in tetraploids than in diploids. The strongest correlation was in cell size. Tetraploid pollen and guard cells were larger than in diploids and the hexaploids showed a correspondingly larger size than the

tetraploids. Another possible size correlation with polyploidy is seen in the two closely related genera *Phalacraea* and *Guevaria*. The former is larger in most parts and has pollen grains ca. 25 μm in diameter. The single chromosome count shows $n = 20$. *Guevaria* is a genus of distinctly smaller plants with pollen grains nearer 20 μm in diameter and chromosome counts of $n = 10$. Variations of pollen size and chromosome number are not notably correlated in other members of the tribe.

Other modifications of pollen are associated with meiotic irregularities. Holmgren (1919) studied the modified development and defective pollen formation in *Eupatorium glandulosum* (= *Ageratina adenophora*), an apomictic species with $2n = 51$. Holmgren recognized the species as a triploid related to *Eupatorium ageratoides* (= *Ageratina altissima*) and *Eupatorium* (*Ageratina*) *purpusii* having chromosome numbers of $n = 17$. *Ageratina riparia* is another weedy, widely adventive species of the genus with reports of $2n = 48$ correlated with defective pollen. Apomixis is common in *Ageratina* and the infrequency of normal sexual reproduction may be a major factor in the development of the more than 200 species. Pollen variation also occurs in other genera of the Eupatorieae but most notably in *Stevia* where as many as four distinct pollen states have been recognized in some species (King & Robinson, 1967). The most common modified state has altered furrow patterns and has a larger size than in normal grains. Grashoff (1972) related such pollen variations directly to irregularities in meiosis. In contrast to *Ageratina*, *Stevia* includes many sexually reproducing populations within its apomictic species, and natural hybridization is frequent between some species (Grashoff, 1972).

Chromosome Numbers and Phylogeny in the Eupatorieae

Previous subtribal concepts have been based primarily on the form of pappus, the ribbing of the achene, and the development of the anther appendage. The four subtribes must now be considered almost totally artificial and useless for phylogenetic comparisons. Traditionally, Ageratinae has included those genera not placed in one of the other subtribes. Piqueriinae contained most but not all of the genera with reduced anther appendages, including *Phania* which is most closely related to *Ageratum*, *Ophryosporus* which is closer to *Critonia*, and *Podophania* which is a *Hofmeisteria*. *Piqueria* itself contained elements belonging to three remotely related groups, *Koanophyllon*, *Ophryosporus*, and *Erythradenia*. The subtribe Kuhniinae, with more numerous ribs on the achenes, contained elements related to *Brickellia* with chromosome complements of $n = 9$; *Liatris*, with mostly $x = 10$; *Carphochaete*, which is more closely related to *Stevia*, with $x = 11$; and *Kanimia*, which is related to *Mikania* with $x =$ mostly 17–20. These genera differ greatly in many morphological characters as well as their cytology. Adenostemmatinae was the smallest subtribe and, with the exclusion of *Hartwrightia*, the only natural one (King & Robinson, 1974a).

Although the previous subtribal concepts are rejected, no new concepts have yet been formalized. Actually, it is at precisely this level of relationships that cytology might prove most helpful and at least some of the evolutionary trends are reflected by cytology. It seems best for the purposes of this study to discuss

the Eupatorieae in terms of cytological groups, starting with the most diverse elements having x = 10 and proceeding through the less numerous groups with $x = 4$, 5, and 9. The treatment concludes with the genera having chromosome numbers higher than $x = 10$, including two major groups with $x = 11$–12 and with $x = 16$–18. See Table 2.

GENERA WITH $X = 10$

Included here is one of the largest complexes in the tribe, having members concentrated in the eastern parts of both North and South America. The members tend to have papillose style branches and corolla lobes, anther collars with strong annulate thickenings, and the pappus setae often with rounded apical cells. In the group is *Eupatorium*, with the related *Eupatoriadelphus*, *Austroeupatorium*, *Stomatanthes* and *Hatschbachiella* (Group II), all of which have pubescent style bases; *Disynaphia*, with the related *Symphyopappus*, *Raulinoreitzia*, *Grazielia* and *Campovassouria* (Group III), all having plain style bases, subimbricate phyllaries, and 5 flowers per head (King & Robinson, 1971d); and the vast group related to *Conoclinium* and *Gyptis*, including *Agrianthus*, *Barrosoa*, *Campuloclinium*, *Conocliniopsis*, *Dasycondylus*, *Lourteigia*, *Neocuatrecasia*, *Tamaulipa*, *Trichogonia*, *Trichogoniopsis*, and *Urolepis* (Group IV) having usually plain style bases, mostly eximbricate phyllaries, and more than 5 flowers per head. The first group in the complex is noteworthy within the tribe for its natural occurrence in the eastern hemisphere, *Eupatorium* reaching Asia and Europe in the north and *Stomatanthes* having 3 species across the Atlantic in Africa. The group including *Gyptis* is notable for its extreme elaboration and predominance in easternmost Brazil. The entire complex, with few exceptions, includes only species with gametic chromosome numbers of $n = 10$ or multiples of 10. About 10 species of *Eupatorium* s. str. from North America and Asia have plants with $n = 15$ in addition to the apparently more common ones of $n = 10$ and $n = 20$. Such numbers supposedly result from hybridization between the different ploidy levels that are common in the genus, and are perpetuated by apomixis. Grant (1953) noticed the small size of the chromosomes of *Conoclinium coelestinum* (L.) DC., but related forms have not been studied for this characteristic.

Ageratum and *Phania* seem related to *Gyptis* but have been separated here into a series of more western genera (Group VI) with reduced pappus. These are morphologically transitional to genera having gametic chromosome numbers of $n = 11$ or 12.

Another major element in the Eupatorieae having $n = 10$ is the assemblage of genera related to *Critonia* (Group XII), with genera such as *Koanophyllon*, *Fleischmanniopsis*, and *Eupatoriastrum* being concentrated in the more tropical parts of Central America, the West Indies, and northern South America. The genera *Austrocritonia* and *Neocabreria* are rather isolated members of this more typical series in southern Brazil, and there is a related complex in the Andes containing *Aristeguietia*, *Asplundianthus*, *Critoniella*, *Cronquistianthus*, and *Ophryosporus*. Members of the complex have phyllaries subimbricate to imbricate, but the group is most notable for its lack of specializations, being difficult to delimit and per-

haps in part artificial. The group of genera including *Critonia* may be related to other genera with a gametic chromosome number of $n = 16$–18 through such genera as *Hebeclinium* which has $n = 10$.

More structurally distinct from *Critonia* but evidently closely related is the *Praxelis* group (XIII), occurring mainly in Brazil. In addition to *Praxelis* the group includes *Praxeliopsis*, *Lomatozoma*, *Eupatoriopsis*, *Eitenia* and the large genus *Chromolaena*, all having involucres that shed all their phyllaries at maturity. *Chromolaena* has a range extending to Mexico and the West Indies where the subgenus *Osmiella* seems to intergrade with some members of the *Critonia* group in the area. *Osmiopsis plumeri* (Urban & Ekman) K. & R. of Haiti has a mixture of *Chromolaena* and *Koanophyllon* floral features not explicable by simple convergent evolution. In spite of marked involucre, corolla, and anther differences, *Chromolaena* of the *Praxelis* group and *Koanophyllon* of the *Critonia* group seem to have retained sufficient cytological similarity to be able to form successful hybrids.

The distinctive group of genera related to *Ayapana* (Group VIII) is largely restricted to South America with a few widely distributed or adventive species. The group is most inadequately represented in cytological studies. The genera *Ayapanopsis*, *Gongrostylus*, *Gymnocondylus*, *Alomiella*, and *Monogerion* have not been counted. Within *Ayapana* itself $n = 17$ has been reported for one species, $n = 8$ and $n = 18$ for another, and a third species is reported here with two counts of $n = 10$. The monotypic *Polyanthina* has been counted once as $n = 12 \pm 1$ and twice as $n = 10$; *Isocarpha* earlier reported as having a gametic chromosome number of $n =$ ca. 8, is now known to have $n = 10$; *Heterocondylus* is reported here as $n =$ ca. 20; and *Condylidium*, which is perhaps more distantly related to the other genera in the series, has $n = 10$. One is inclined even on the basis of this small sample to suggest a base number of $x = 10$ for the group, although the situation in *Ayapana* itself, with about a dozen species, should be clarified. Certainly, other characters show the group has no close relationship with others having chromosome numbers $n = 11$, 12, 17 or 18.

Liatris and the related genera, *Carphophorus*, *Garberia*, *Litrisa*, and *Trilisa* of the southeastern United States (Group X) have a basic chromosome number of $x = 10$, with polyploidy only in *Liatris*. Among the diploid series of *Liatris* (Gaiser, 1949, 1950a, 1950b), Spicatae and Pycnostachyae exhibited variation in chromosome length, with some medium and long chromosomes with subterminal constrictions, whereas Graminifoliae and Pauciflorae have more uniform karyotypes. Polyploidy occurs in series Punctatae and has been important in the evolution of species in this group.

GENERA WITH $N = 4$

The genus *Fleischmannia* (Group XI) has many features of the *Gyptis* relationship but differs by several important details including the usually subimbricate involucre and the unique form of papillae on the corolla. Similarity of habit has caused confusion with some species of *Ageratina*, but the latter genus is strikingly distinct in floral anatomy and cytology (King & Robinson, 1970a, 1970b). Most specimens of *Fleischmannia* that have been counted have $n = 10$ or mul-

TABLE 2. General distribution, habit, and chromosome number of genera of Eupatorieae.

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
		I. Adenostemmatinae				
Adenostemma	pantropical	P	20	4	10, 5	
		II. Eupatoriinae				
Eupatorium	e. U.S., Asia, Eur.	P	38	20	10, 15, 20	yes
Eupatoriadelphus	e. North Amer.	P	4	4	10, 20	yes
Austroeupatorium	S. Amer., advent.	P,S?	11	2	10	
Stomatanthes	Brazil, Africa	P	15	1	10	
		III. Disynaphia Group				
Campovassouria	s. Brazil, Parag., Urug., n. Argent.	P	1	1	10	
Disynaphia	Brazil, Uruguay	P	12	1	10	
Grazielia	Brazil	P	9	1	10	
Raulinoreitzia	Brazil	P	2	1	10	
Symphyopappus	Brazil	P	13	2	10	
		IV. Gyptis Group				
Barrosoa	S. America	P	11	1	10	
Campuloclinium	Cent. Amer. to Brazil	P	20	1	10	
Conocliniopsis	S. America	P	1	1	10, 30	yes
Conoclinium	U.S., Mexico	P	3	3	10	
Gyptis	Brazil	P	7	1	30	
Lourteigia	Colombia, Venezuela	P	7	2	10	
Tamaulipa	Texas, n. Mexico	P	1	1	10	
Trichogoniopsis	Brazil	P	2	1	10	
Vittetia	Brazil	P	1	1	10	
		V. Acritopappus Group				
Acritopappus	Brazil	S	3	1	9	
		VI. Piqueria Group				
Ageratum	trop. Amer., advent.	P	43	14	10, 15, 20	yes
Ascidiogyne	Peru	P	1	1	10	

TABLE 2. (Continued).

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
Carphochaete	sw. U.S., Mexico	S	5	2	11	
Cronquistia	Mexico	P	1	1	12	
Guevaria	Ecuador, Peru	P,sS	4	2	10	
Microspermum	Mexico	P	7	3	12	
Phalacraea	Colombia to Peru	P	5	1	20	
Piqueria	Mex., C. Amer., W. Ind.	P	7	2	12, 25	yes
Stevia	Mex., C. Amer., S. Amer.	A,P,S	150–200	37	11, 12, ca. 30 $2n = 24$, 33, 34, 36, ca. 43, 46, 40–47 var, $2\text{–}8_{II} + 30\text{–}18_{I}$	yes
		VII. Trichocoronis Group				
Trichocoronis	Texas, Mexico	P	2	1	15	
Sclerolepis	e. U.S.	P	1	1	15	
Shinnersia	Texas, Mexico	P?	1	1	ca. 30	
		VIII. Ayapana Group				
Ayapana	W. Ind., S. Amer., advent.	P	11	3	8, 10, 17, 18	yes
Condylidium	C. Amer., W. Ind., n. S. Amer.	P	2	1	10	
Heterocondylus	C. Amer., S. Amer.	P,S	12	1	ca. 20	
Isocarpha	trop. Amer.	P	12	2	10	
Polyanthina	Costa Rica, n. S. Amer.	P	1	1	10, $(12 \pm 1?)$	
		IX. Alomiinae				
Barroetia	Mexico	P	6	3	9	
Brickellia	mostly sw. U.S., Mex., Central America	A,P,S	100	51	9	
Brickelliastrum	sw. U.S.	P	1	1	10	
Carminatia	Mexico	P	2	1	10	
Crossothamnus	Peru	S	1	1	10	
Malperia	sw. U.S., Mexico	P	1	1	10	
Phanerostylus	n. Mexico	sS	3	1	9	
Pleurocoronis	sw. U.S., w. Mexico	sS	3	2	9	

TABLE 2. (Continued).

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
		X. Liatris Group				
Carphephorus	se. U.S.	P	5	4	10	
Garberia	Florida	S	1	1	10	
Liatris	se. U.S.	P	34	20	10, 20, 30	yes
Litrisa	se. U.S.	P	1	1	10	
Trilisa	se. U.S.	P	2	2	10	
		XI. Fleischmannia Group				
Fleischmannia	N. Amer., w. S. Amer. advent.	A,P	75	10	10, 4, 20, 29, 30	yes
		XII. Critonia Group				
Aristeguietia	Andes	S	20	4	10	
Asplundianthus	n. S. Amer.	S	9	1	10	
Austrocritonia	Brazil	S	3	1	10	
Critonia	C. Amer., W. Ind., n. S. Amer.	P,S,T	33	4	10	
Critoniella	Colombia, Venezuela	P	5	1	10	
Koanophyllon	trop. Amer.	P,S	109	5	10, 20	yes
Ophryosporus	S. Amer.	P,S	38	1	10	
		XIII. Praxelis Group				
Chromolaena	trop. Amer., advent.	P,S	over 130	11	10, 29	yes
Praxelis	S. Amer.	P	13	1	$2n = 48$, 51, ca. 80 20 ($7_{II} + 26_{I}$)	
		XIV. Hebeclinium Group				
Bartlettina	trop. N. & S. Amer.	P,S	20	5	10, 16	
Decachaeta	Mex., Cent. Amer.	S	7	1	16	
Hebeclinium	mostly S. Amer., 1 trop. Amer.	P,S	18	4	10	

TABLE 2. (Continued).

Genus	General distribution	Habit	Approx. no. of species	No. of species counted	Gametic chromosome numbers	Polyploidy
Matudina	s. Mexico	P,S	1	1	16	
Peteravenia	Mex., Cent. Amer.	P,S	4	1	10, ca. 17?	?
		XV. Neomirandea Group				
Neomirandea	Mex., C. Amer., n. S. Amer.	S	24	5	17, 20, ca. 24, 25	
		XVI. Mikania Group				
Mikania	trop. Amer., Africa, trop. Asia	P,Li,S	300	13	ca. 16, 17, 18, 19, 20, $2n = 34$–38	
		XVII. Ageratina Group				
Ageratina	N. & C. Amer., W. Ind., w. S. Amer., advent.	P,S	230	38	ca. 16, 17, 18, 20, ca. 25, ca. 40, ca. 42, 48, $2n = 48$, 50, 51, 55–2 frag., 68–69, ca. 80, ca. 85	yes
Oxylobus	Mex., n. S. Amer.	S	5	4	16	
		XVIII. Hofmeisteria Group				
Hofmeisteria	Mexico	P,S	8	1	18, 19	

tiples of that number. Various authors including Turner & King (1964) and Baker (1967) have reported $n = 4$ in two annual species of the genus, *F. sinclairii* and *F. microstemon*. Baker regards the lower number as derived and states: "This is suggested by the fact that the chromosomes of the four-paired cytotype are much larger than those of the ten-paired form and by the behavior of the hybrid between them (with $2n = 14$). At the first meiotic division of the pollen mother cells in this hybrid the commonest configuration to be seen is of four multivalents (or at least bivalents) involving the four large chromosomes of the four-paired cytotype, together with an appropriate number of univalents. This is consistent with an evolution of the four-paired condition by gradual reduction of the chromosome number by unequal translocations followed by loss of centromeres on the classic *Crepis* model (Tobgy, 1943). The asymmetry of the chromosomes in the four-paired plants is also in keeping with this ancestry." Recent revisions have shown that all specimens with $n = 4$ were *F. microstemon* and that *F. sinclairii*, which has $n = 10$ exclusively is not so closely related, having differences in leaf texture, size of heads, shape and pubescence of phyllaries, and in the form and color of the achenes. More recently, Grashoff et al. (1972) have reported $n = 4$ from *F. hymenophyllum*, a large probably perennial herb from Costa Rica and Panama that shows no particular relationship to *F. microstemon*. In spite of the lower numbers in two species, the original basic chromosome number of *Fleischmannia* seems to have been $n = 10$.

Recent reidentifications have also provided a revised concept for *Fleischmannia pycnocephala*, which is now seen to include only plants with $n = 20$, $n = 30$ and variants in Guatemala reported in this study as $n =$ ca. 40 and $n = 42$–44 with 2–4_I. Many previous reports belong to related species, especially *F. pratensis* which has $n = 20$. The resegregated *F. sonorae* (A. Gray) K. & R. of Sonora and Arizona resembles *F. incarnata* (Walter) K. & R. of the eastern United States and *F. seleriana* (B. L. Robinson) K. & R. of the eastern escarpment of Chiapas and Veracruz in having $n = 10$.

GENERA WITH $N = 5$

This low count has been reported once by Turner & Irwin (1960, as *Adenostemma brasiliense*) for a specimen now determined as *Adenostemma involucratum* K. & R. Four other species including the true *A. brasiliense* (Pers.) Cass. and *A. platyphyllum* Cass. (once as *A. lavenia*) are reported as $n = 10$. Turner and Irwin have suggested that $n = 5$ is the basic chromosome number for the genus, but in context, reduction from $n = 10$ in this single species appears more probable. The closely related genera *Sciadocephala* and *Gymnocoronis* have not been counted. The subtribe Adenostemmatinae (Group I) is one of the most distinctive elements of the Eupatorieae but the characteristic viscid knobs of the achenes and unsclerified interstices of the receptacle indicate a specialized rather than primitive position in the tribe.

GENERA WITH $X = 9$

The primary group of Eupatorian genera having chromosome counts of $n = 9$ has been studied extensively by Gaiser (1953, 1954) who studied 41 species of

Brickellia, 4 of *Kuhnia*, and 2 of *Barroetia* (Group IX). *Brickellia* has long been recognized as distinct, but exact limits have been so uncertain that Correll & Johnston (1970) have suggested possible reduction of the genus and *Mikania* to synonymy under *Eupatorium*. Harcombe & Beaman (1967), in a different approach, have abandoned the morphological characters and have delimited the genus on the basis of the distinctive $n = 9$ chromosome number. In reality, the *Brickellia* group is much more extensive than previously realized, being characterized by the usually very long and clavate style branches and a usually narrow corolla opening. The group includes genera such as *Helogyne*, *Leptoclinium*, and *Dissothrix* of South America, as well as many distinctive segregates previously placed in *Brickellia* or *Eupatorium*. Many of the genera, including *Asanthus*, *Flyiella*, *Alomia*, *Dyscritogyne*, *Kyrsteniopsis*, and *Steviopsis* of Mexico are not known cytologically. Among the genera that have been studied, the gametic chromosome number $n = 9$ has been characteristic of *Brickellia* (including *Kuhnia*), *Barroetia*, *Phanerostylis*, and *Pleurocoronis*. The number has not been reported yet for any of their strictly South American relatives. The gametic chromosome number n = 10 has been reported, however, from a number of related genera including *Malperia* (Raven in King, 1967a), *Brickelliastrum* (Watson, 1973, as *Brickellia*), and *Carminatia* of North America, as well as *Crossothamnus* (Turner et al., 1967, as *Eupatorium weberbaueri*) and *Austrobrickellia* (Krapovickas, 1951, as *Eupatorium patens*) from South America. The distribution of numbers suggests a derivation of $n = 9$ from the more characteristic Eupatorian $n = 10$ within the *Brickellia* group.

Two counts of $n = 9$ are available for the genus *Acritopappus* (Group V) [Coleman, 1970, as *Alomia longifolia* (Gardn.) B. L. Robinson]. Interpretation is difficult because relationships of the genus are not clear. There is some resemblance to the as yet uncounted *Radlkoferotoma* and there may be some relation to the *Gyptis* group in spite of the subimbricate phyllaries. *Acritopappus* is definitely not closely related to other members of the tribe having $n = 9$, and we presume that the chromosome number of this genus has been derived independently from $n = 10$.

GENERA WITH $x = 11$ OR 12

The known genera having $n = 11$ or 12 appear to be part of a larger group having strongly papillose corolla lobes and annulate thickenings in the cells of the anther collars (Group VI). The group shows a strong tendency for pappus reduction with squamiform and coroniform types represented. These features and chromosomal evidence both suggest strongly that the genera are related to one another and have no direct relationship to those with gametic chromosome numbers of $n = 16$–18.

In the group of genera with a gametic chromosome number of $n = 11$ or 12, *Stevia* and *Carphochaete* seem closely related as suggested by Turner (1959). The single species of *Cronquistia*, reported here as having $n = 12$, was originally described as a *Stevia* and has more recently been associated with *Carphochaete* (Grashoff, unpublished). Each of the three genera has its own distinctive style structure, with *Carphochaete* ($n = 11$) especially remarkable, indicating that

stylar morphology alone is not a reliable indication of relationship. *Stevia* has been extensively treated cytologically by Grashoff (Grashoff et al., 1972) with the conclusion that shrubby species all have a gametic chromosome number of $n = 12$; herbaceous species with laxly paniculate arrangement of capitula have $n = 11$ with no aneuploidy; and herbaceous species with compact-corymbose arrangements of capitula mostly have $2n = 34$ univalents with considerable aneuploidy. The great variation and widespread apomixis in *Stevia* allows for interpretation of $2n = 33$ and $2n = 34$ as triploid derivatives of $n = 11$. There is some tendency, however, to interpret the $2n = 34_{I}$ found in *Stevia* as a potential $n = 17$ partly because of the common occurrence of $n = 17$ elsewhere in the tribe. Grashoff reports S. *jorullensis* H.B.K. as having $2n = 17_{II}$ and 34_{I} and S. *plummerae* var. *durangensis* as having $2n =$ ca. 17_{II}, and he suggests that among the compact-corymbose herbaceous species the alternate leaved species "may have numbers based on 11, 12, or 17 within the same species," while "the opposite leaved species appear to be based on $x = 17$ alone." Nevertheless, Grashoff does report the opposite leaved species S. *origanoides* as having both 34 univalents and 43 ± 1 univalents and Keil & Stuessy (1975) have since reported S. *origanoides* as having $n = 11$ and another opposite-leaved species S. *plummerae* var. *durangensis* as having $n = 44_{I}$. Such evidence and the lack of a close relationship of *Stevia* to any of the genera with $n = 17$ indicates that the counts for the genus should be interpreted on the basis of the known $n = 11$ and $n = 12$ numbers that are common in the genus and in related genera. Such reports as the $2n = 17_{II}$ in S. *jorullensis* and $2n =$ ca. 17_{II} in S. *plummerae* var. *durangensis* could be interpreted as the result of preferential pairing, although more observations would be highly desirable. In any case, the three elements within *Stevia* definitely seem, on the basis of overwhelming morphological and anatomical evidence, to be closely related to one another.

Reexamination of the microstructure of the genus *Macvaughiella* shows that the genus is related to the *Stevia* group rather than to the *Ageratina* group where it was recently placed (King & Robinson, 1970b). There is only an unpublished chromosome count of $n =$ ca. 13 by R. C. Jackson for *M. mexicana* (Sch. Bip.) K. & R. (MEXICO. CHIAPAS: 7 mi N of Arriaga, *Cronquist & Sousa 10459*).

Piqueria s. str. has a base chromosome number of $x = 12$ (25) and shares with *Stevia* the characteristic reduced number of flowers, equal to the number of phyllaries. *Microspermum* also seems related and Rzedowski (1970) has reviewed the cytology of 3 species, all having $n = 12$. A number of genera in South America resemble *Piqueria* and seem to be related. Thus far, however, all chromosome counts for these genera have been on a base of $x = 10$; *Ascidiogyne*, $n = 10$, *Phalacraea*, $n = 20$, and *Guevaria*, $n = 10$. Some close relatives of *Guevaria* remain uncounted, including *Ellenbergia* and *Ferreyrella* of the Andes, *Piqueriella* of eastern Brazil, and *Piqueriopsis* of western Mexico. The counts of $n = 10$ might reflect phyletic ties with the structurally similar widely distributed genus *Ageratum*, and the latter shows significant features in common with the *Gyptis* group. *Ageratum* has been reviewed by Johnson (1971) and has a basic chromosome number of $x = 10$. *Ageratum micropappum* Baker is a questionable member in

the genus which lacks the characteristic conical receptacle. The species has been counted as $n = 9$. [BRAZIL. BAHIA: *Coleman 501* (Coleman, unpublished)].

The pattern of distribution of chromosome numbers and the interpretation of the structural evidence indicate that $n = 11$ and $n = 12$ in the present group have been derived by aneuploid increase within the group from $n = 10$, which is common both in this assemblage of genera and in other parts of the tribe.

GENERA WITH $N = 15$

The number has been obtained from various species of *Eupatorium* and from one plant of *Ageratum*, in both, it is almost certainly the result of hybridization between the more common populations with $n = 10$ and $n = 20$, and it could persist as a result of asexual reproduction. Otherwise the number is known in the tribe from members of the *Trichocoronis* group (VII). A single count is available for one of the two species of the genus *Trichocoronis* of the southwestern U.S. and central Mexico. *Trichocoronis* seems to be related to the recent taxonomic segregate *Shinnersia*. The many structural differences in the latter might be correlated with its extreme aquatic nature. A count of $n =$ ca. 30 has been obtained for *Shinnersia* by Chambers (King & Robinson, 1970c). This number could be a multiple of either 10 or 15 and leaves the base number of the group still in doubt. *Sclerolepis* is reported here as $n = 15$ and ca. 30.

GENERA WITH $X = 16$–18

The genera of this complex are variable in many features and comprise a number of distinct elements. The complex shows some common trends, however, that seem to preclude close relation to the genera with $n = 11$ and $n = 12$, a comparatively homogeneous assemblage. The cells of the anther collars are nearly or completely without annular thickenings and the corolla lobes of all but the *Ageratina* group lack papillae. The pappus is present and capillary in all but *Oxylobus* and *Erythradenia*. One specialization of the pappus is the tendency for fragile and deciduous setae in members of both the *Hebeclinium* and *Ageratina* groups.

The most significant result of the new reports in this paper is the recognition and partial clarification of a group of related genera (Group XIV) with many Mexican and Central American species having a gametic chromosome number of $n = 16$. The present report of $n = 16$ is the first for *Decachaeta*, a genus previously noted as a close relative of *Bartlettina*. Four species of *Bartlettina* are also reported here with a gametic chromosome number of $n = 16$. One of the four species, *B. sordida*, has been reported previously as $2n = 20$ by Holmgren (1919, as *Eupatorium ianthinum*) but the Holmgren identification has not been confirmed. Also, one *Bartlettina* from South America has been reported as having $n = 10$ (Powell & Cuatrecasas, 1970, as *Critonia paezense*) but the South American members of the genus are aberrant in a number of other details and seem at least subgenerically distinct. The number reported here for *Matudina* seems to confirm its relationship to *Bartlettina* and *Decachaeta*. In the original description of the single species of *Matudina*, McVaugh (1972, as *Eupatorium corvi*)

made comparison with species placed in *Eupatoriastrum* s. str., for which no chromosomal information is available. *Eupatoriastrum*, although superficially similar to *Matudina*, is closely related to *Koanophyllon* in the *Critonia* series in which there is a base of $x = 10$. A probable close relative of *Bartlettina* is *Peteravenia*. In the latter only one of the four species has been examined cytologically, with two populations from central Chiapas having $n = 10$, a third collection from the same general area having $n =$ ca. 17 (20?), suggesting a probable basic chromosome number of $x = 10$ for the genus. An undoubted relative of *Bartlettina* is the primarily South American genus *Hebeclinium* which is uniformly reported as having $n = 10$. The gametic chromosome number of $n = 16$ in *Decachaeta*, *Matudina*, and at least 4 of the approximately 20 species of *Bartlettina* could be most easily derived by aneuploid reduction from $n = 20$. It is probable but not certain that the $n = 16$ in the three genera was derived from a single common ancestor having that number.

The genus *Neomirandea* (Group XV) consists of two rather distinctive but related elements. The subgenus *Critoniopsis* is known by counts of $n = 17$. The subgenus *Neomirandea* has a variety of reports indicating $n = 20$ and $n = 25$. The occurrence of these numbers might be an indication of multiples of $x = 5$ which seem to occur in scattered and isolated places in the tribe, or might have originated as a result of hybridization between plants with $n = 20$ and a putative $n = 30$. The cytological groups correlate completely with the subgeneric classification based on style bases and to some extent on corolla pubescence. The present counts include 3 species of subgenus *Neomirandea* representing its two major variations and many specimens of 2 species of subgenus *Critoniopsis*. Studies of the anatomy have given the distinct impression that subgenus *Neomirandea* of this mostly epiphytic genus is the derived element, even though it contains those species noted as terrestrial on labels. Recent field work shows that the supposedly terrestrial species are all restricted to rich humus substrates and often possess distinctive prop-root systems. Within the context of the tribe, however, it would seem that $n = 20$ would be the original basic number in the genus and $n = 17$ would be derived.

Mikania (Group XVI) and the weak segregate *Kanimia* have counts of $n =$ 17, 18, and 19 with a few additional reports of $n =$ ca. 16 and $n =$ ca. 20. There are varied reports in a number of species, and it is uncertain how much is real variation or how much is the result of the staining difficulties often noted in attempts to count chromosomes in *Mikania*. The two counts of $n =$ ca. 19 reported here for *M. scandens* represent the first for this endemic eastern North American species. Previous counts reported under this name represent related species that are sometimes included under a broader concept.

The largest genus of the tribe may ultimately prove to be *Ageratina*, and it includes the majority of species of the tribe for which $n = 17$ has been reported. Such counts have been regularly obtained for members of the genus from both North and South America. There is apomixis in the genus and a few species are evidently polyploid. One, *A. aschenborniana* (Schauer) K. & R. seems to include at least two cytotypes respectively with $n = 17$ and $n = 20$. The recent report of $n = 10$ by Grashoff et al. (1972) is less explicable. The specimen at the Univer-

sity of Texas thus annotated has a different collection number from that reported in the publication and might be held suspect. A new report of $n =$ ca. 10 in this study suggests again, however, that some lower numbers occur in the species. Three species of the northern Andes, *A. exerto-venosa* (Klatt) K. & R., *A. pseudochilca* (Benth.) K. & R., and *A. tinifolia* (H.B.K.) K. & R., belong to a distinctive group that is restricted to that area. Reports of *A. tinifolia* by Powell & King (1969) and reports of the other two in this paper show consistently $n =$ ca. 40, $n =$ ca. 40 + B chromosomes, or $n =$ ca. 42. Such numbers are not easily derived from $n = 17$ but might reflect a more basic $n = 20$ for the group.

Ageratina is the largest of a group of closely related genera including *Oxylobus*, *Piptothrix*, *Jaliscoa*, and *Spaniopappus* (Group XVII). *Oxylobus*, which differs from *Ageratina* in only one significant structure, the pappus, is nevertheless consistently reported as having $n = 16$. The chromosome number thus seems to confirm the conclusions based on anatomical features that *Oxylobus* is related closely to *Ageratina* rather than to *Ageratum* with $x = 10$ or to *Stevia* with $x = 11$ and 12. Structure would also dictate that the *Bartlettina-Decachaeta* series with $n = 16$ is sufficiently distinct to indicate an independent origin for the number in that group.

The great differences among the species with mostly $n = 16$–18 does not preclude the possibility that one very large and complex natural group may be involved. The *Bartlettina* series is not very different in some of its basic structures from subgenus *Critoniopsis* of *Neomirandea*. *Neomirandea* in turn shares a tendency for epiphytism and large quadrate corolla cells with *Mikania*. *Neomirandea* might also prove to be linked with *Ageratina* through such intermediates as the poorly known and possibly extinct *Standleyanthus*. In the context of the tribe the chromosome numbers in these genera were probably derived by aneuploid reduction from $n = 20$ which is still represented sporadically in the group.

GENERA WITH $N = 18$ AND 19

Hofmeisteria forms a very distinct element in the tribe Eupatorieae (Group XVIII), and there is no basis for association with the group of genera which primarily have $n = 16$–18. *Hofmeisteria* seems most likely derived independently from ancestors having $n = 20$. Both $n = 18$ and $n = 19$ in *Hofmeisteria* are based upon reports from a single species, and further information would be highly desirable.

No likely ancestor is evident for *Hofmeisteria*, but its remote position recalls two other genera of a unique group, *Oaxacania* and *Carterothamnus*. It is these last two genera that possess the most primitive form of paleae in the tribe and which are most clearly in need of cytological investigation.

General Speculation on Numbers

The overall distribution of chromosome numbers in the Eupatorieae indicates that the most likely original base number for the ancestor of the tribe was $n = 10$. Almost certainly reduction has occurred in *Fleischmannia* and *Adenostemma* to $n = 4$ and $n = 5$, respectively. Additional aneuploid reduction in chromosome

number seems to have occurred in the ancestory of *Brickellia*, *Acritopappus*, and a few other genera with $n = 9$, and also in the derivation of genera with $n =$ 19, 18, 17, and 16. Plants with $n = 15$ seem to have been derived by hybridization between those with $n = 10$ and others with $n = 20$, in many cases followed by apomixis. The interpretation of $n = 25$ in *Neomirandea*, on the other hand, is more difficult. The possibility that some genera with $n = 19$, 18, 17, and 16 may have been derived from diploid parents with chromosome numbers lower than $n = 10$ cannot be excluded for all genera, but few such diploids are known, and none that are directly related to the plants with higher numbers.

In a single species of *Peteravenia*, both $n = 10$ and $n =$ ca. 17 are known, and, if the latter number can be confirmed, aneuploid reduction within the genus would be indicated. Four species of *Bartlettina* have $n = 16$, a fifth $n = 10$, and a similar relationship may be suspected for it. In any case, in the *Hebecliniium-Bartlettina* group the two numbers $n = 10$ and $n = 16$ seem well established in different members of a closely related group.

There seem to be no problems in the interpretation of a separate series in the *Piqueria-Stevia* relationship showing aneuploid gain from $n = 10$ to $n = 11$ and 12.

Recent studies of structural diversity, cytology, and phytogeography of the Eupatorieae have seemed to indicate a tribe much more diverse than previously published treatments would allow. The complexity of the new classification is considered a reflection of a complex phylogeny for the tribe, many parts of which seem to be very actively evolving.

Literature Cited

Anderson, L. C., D. W. Kyhos, T. Mosquin, A. M. Powell & P. H. Raven. 1974. Chromosome numbers in Compositae IX. *Haplopappus* and other Astereae. Amer. J. Bot. 61: 665–671.

Baker, H. G. 1967. The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. Taxon 16: 293–300.

Bennett, M. D. 1972. Nuclear DNA content and minimum generation time in herbaceous plants. Proc. Roy. Soc. London, Ser. B, Biol. Sci. 181: 109–135.

Coleman, J. 1968. Chromosome numbers in some Brazilian Compositae. Rhodora 70: 228–240.

———. 1970. Additional chromosome numbers in Brazilian Compositae. Rhodora 72: 94–99.

Correll, D. S. & M. C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, Texas.

Gaiser, L. O. 1949. Chromosome studies in *Liatris*. I. Spicatae and Pycnostachyae. Amer. J. Bot. 36: 122–135.

———. 1950a. Chromosome studies in *Liatris*. II. Graminifolia and Pauciflorae. Amer. J. Bot. 37: 414–423.

———. 1950b. Chromosome studies in *Liatris*. III. Punctatae. Amer. J. Bot. 37: 763–777.

———. 1953. Chromosome studies in Kuhniinae (Eupatorieae) I. *Brickellia*. Rhodora 55: 253–267, 269–288, 297–321, 328–345.

———. 1954. Studies in the Kuhniinae (Eupatorieae). II. J. Arnold Arbor. 35: 87–133.

Grant, W. F. 1953. A cytotaxonomic study in the genus *Eupatorium*. Amer. J. Bot. 40: 729–742.

Grashoff, J. L. 1972. A systematic study of the North and Central American species of *Stevia*. Ph.D. dissertation, Univ. of Texas, 609 pp.

———, M. W. Bierner & D. K. Northington. 1972. Chromosome numbers in North and Central American Compositae. Brittonia 24: 379–394.

Harcombe, P. A. & J. H. Beaman. 1967. Transfer of two Mexican species from *Eupatorium* to *Brickellia* (Compositae). Southw. Naturalist 12: 127–133.

HOLMGREN, I. 1919. Zytologische Studien über die Fortpflanzung bei den Gattungen *Erigeron* und *Eupatorium*. Kongl. Svenska Vetenskapsakad. Handl. 59(7): 1–118.

JOHNSON, M. F. 1971. A monograph of the genus *Ageratum* L. (Compositae-Eupatorieae). Ann. Missouri Bot. Gard. 58: 6–88.

KEIL, D. J. & T. F. STUESSY. 1975. Chromosome counts of Compositae from the United States, Mexico, and Guatemala. Rhodora 77: 171–195.

KING, R. M. 1967a. Studies in the Eupatorieae (Compositae), I–III. Rhodora 69: 35–47, 240.

———. 1967b. Studies in the Eupatorieae, (Compositae) IV. Rhodora 69: 352–371.

——— & H. ROBINSON. 1967. Multiple pollen forms in two species of the genus *Stevia* (Compositae). Sida 3: 165–169.

——— & ———. 1969. Studies in the Eupatorieae (Compositae). XVI. A monograph of the genus *Decachaeta* DC. Brittonia 21: 275–284.

——— & ———. 1970a. Studies in the Eupatorieae (Compositae). XVIII. New combinations in *Fleischmannia*. *Phytologia* 19: 201–207.

——— & ———. 1970b. Studies in the Eupatorieae (Compositae). XIX. New combinations in *Ageratina*. Phytologia 19: 208–229.

——— & ———. 1970c. Studies in the Eupatorieae (Compositae). XII. A new genus *Shinnersia*. Phytologia 19: 297–298.

——— & ———. 1970d. Studies in the Eupatorieae (Compositae). XXVI. A new genus *Austroeupatorium*. Phytologia 19: 433–435.

——— & ———. 1970e. Studies in the Eupatorieae (Compositae). XXVIII. The genus *Praxelis*. Phytologia 20: 193–195.

——— & ———. 1970f. Studies in the Eupatorieae (Compositae). XXX. The genus *Ayapana*. Phytologia 20: 210–212.

——— & ———. 1971a. Studies in the Eupatorieae (Compositae). XXXIII. The genus *Gyptis*. Phytologia 21: 22–25.

——— & ———. 1971b. Studies in the Eupatorieae (Asteraceae). XXXVII. The genus *Hebeclinium*. Phytologia 21: 298–301.

——— & ———. 1971c. Studies in the Eupatorieae (Asteraceae). XLVIII. The genus *Critonia*. Phytologia 22: 46–51.

——— & ———. 1971d. Studies in the Eupatorieae (Asteraceae). LI. The Disynaphioid complex. Phytologia 22: 109–110.

——— & ———. 1972a. Studies in the Eupatorieae (Asteraceae). LXXVIII. A new genus *Brickelliastrum*. Phytologia 24: 63–64.

——— & ———. 1972b. Studies in the Eupatorieae (Asteraceae). XCI. A new genus *Macropodina*. Phytologia 24: 173–175.

——— & ———. 1972c. Studies in the Eupatorieae (Asteraceae). C. A key to the genera of Nueva Galicia, Mexico. Phytologia 24: 267–280.

——— & ———. 1972d. Studies in the Eupatorieae (Asteraceae). CIII. A new genus *Ayapanopsis*. Phytologia 24: 382–386.

——— & ———. 1973. Studies in the Eupatorieae (Asteraceae). CXIV. The genera of Barro Colorado Island, Panama. Phytologia 27: 233–240.

——— & ———. 1974a. Studies in the Eupatorieae (Asteraceae). CXXVII. Additions to the American and Pacific Adenostemmatinae. *Adenostemma*, *Gymnocoronis*, and *Sciadocephala*. Phytologia 29: 1–20.

——— & ———. 1974b. Studies in the Eupatorieae (Asteraceae). CXXXI. A new genus *Guevaria*. Phytologia 29: 257–263.

——— & ———. 1975a. Studies in the Eupatorieae (Asteraceae). CXLII. A new genus *Badilloa*. Phytologia 30: 229–234.

——— & ———. 1975b. Eupatorieae. *In* R. E. Woodson, Jr. & R. W. Schery, Flora of Panama. Ann. Missouri Bot. Gard. 62: 888–1004. [1976].

KRAPOVICKAS, A. 1951. Numeros cromosomicos de tres compuestas riojanas. Bol. Soc. Argent. Bot. 4: 105–106.

MCVAUGH, R. 1972. Compositarum Mexicanarum Pugillus. Contr. Univ. Michigan Herb. 9: 359–484.

ORNOUFF, R., P. H. RAVEN, D. W. KYHOS & A. R. KRUCKEBERG. 1963. Chromosome numbers in Compositae. III. Senecioneae. Amer. J. Bot. 50: 131–139.

———, T. MOSQUIN, D. W. KYHOS & P. H. RAVEN. 1967. Chromosome numbers in Compositae. VI. Senecioneae. II. Amer. J. Bot. 54: 205–213.

PAYNE, W. W., P. H. RAVEN & D. W. KYHOS. 1964. Chromosome numbers in Compositae IV. Ambrosieae. Amer. J. Bot. 51: 419–424.
POWELL, A. M. & J. CUATRECASAS. 1970. Chromosome numbers in Compositae: Colombian and Venezuelan species. Ann. Missouri Bot. Gard. 57: 374–379.
——— & R. M. KING. 1969. Chromosome numbers in the Compositae: Colombian species. Amer. J. Bot. 56: 116–121.
———, D. W. KYHOS & P. H. RAVEN. 1974. Chromosome numbers in Compositae. X. Amer. J. Bot. 61: 909–913.
RAVEN, P. H. & D. W. KYHOS. 1961. Chromosome numbers in Compositae. II. Helenieae. Amer. J. Bot. 48: 842–850.
———, O. T. SOLBRIG, D. W. KYHOS & R. SNOW. 1960. Chromosome numbers in Compositae. I. Astereae. Amer. J. Bot. 47: 124–132.
RZEDOWSKI, J. 1970. Estudio sistematico del genero *Microspermum* (Compositae). Bol. Soc. Bot. México. 31: 49–107.
SOLBRIG, O. T., L. C. ANDERSON, D. W. KYHOS, P. H. RAVEN & L. RUDENBERG. 1964. Chromosome numbers in Compositae V. Astereae II. Amer. J. Bot. 51: 513–519.
———, ———, ——— & ———. 1969. Chromosome numbers in Compositae. VII. Astereae III. Amer. J. Bot. 56: 348–353.
———, D. W. KYHOS, A. M. POWELL & P. H. RAVEN. 1972. Chromosome numbers in Compositae. VIII. Heliantheae. Amer. J. Bot. 59: 869–878.
STROTHER, J. L. 1976. Chromosome studies in Compositae. Amer. J. Bot. 63: 247–250.
TOBGY, H. A. 1943. A cytological study of *Crepis fuliginosa*, *C. neglecta*, and their F_1 hybrids and its bearing on the mechanism of its phylogenetic reduction in chromosome number. J. Genet. 45: 67–111.
TOMAN, J., J. HARMATHA & L. NOVOTNY. 1968. Verwandschaftsbeziehungen der Gattung *Adenostyles* and die Berechtigung ihrer Einreihung in die Tribus Senecioneae. Preslia 40: 122–132.
TURNER, B. L. 1959. Meiotic chromosome counts for 12 species of Texas Compositae. Brittonia 11: 173–177.
——— & H. S. IRWIN. 1960. Chromosome numbers in the Compositae. II. Meiotic counts for fourteen species of Brazilian Compositae. Rhodora 62: 122–126.
——— & R. M. KING. 1964. Chromosome numbers in the Compositae. VIII. Mexican and Central American species. Southw. Naturalist 9: 27–39.
———, W. L. ELLISON & R. M. KING. 1961. Chromosome numbers in the Compositae. IV. North American species, with phyletic interpretations. Amer. J. Bot. 48: 216–223.
———, A. M. POWELL & J. CUATRECASAS. 1967. Chromosome numbers in Compositae. XI. Peruvian species. Ann. Missouri Bot. Gard. 54: 172–177.
———, ——— & T. J. WATSON. 1973. Chromosome numbers in Mexican Asteraceae. Amer. J. Bot. 60: 592–596.
WATSON, T. J. 1973. Chromosome numbers in Compositae from the Southwestern United States. Southw. Naturalist 18: 117–124.

NOTE ADDED IN PROOF

Keil and Pinkava (1976) have recently reported a chromosome count of $n = 9$ for *Carminatia*, claimed glabrous style bases for two species of *Brickellia* s. str., and placed *Carminatia* in the synonymy of *Brickellia*. More recently Keil and Pinkava (1977) have corrected these errors and reported $n = 10$ for *Carminatia*.

KEIL, D. J. & D. J. PINKAVA. 1976. Chromosome counts and taxonomic notes for Compositae from the United States and Mexico. Amer. J. Bot. 63: 1393–1403.
——— & ———. 1977. Reinstatement of *Carminatia* DC. (Compositae: Eupatorieae). Phytologia 35: 323.

NEW OR NOTEWORTHY CHROMOSOME RECORDS IN THE ANGIOSPERMS[1, 2]

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ABSTRACT

The following chromosome numbers are reported: *Miersia chilensis* $2n = 20$, *Gethyum atropurpureum* $2n = 14$ (Alliaceae); *Aextoxicon punctatum* $2n = 32$ (Aextoxicaceae); *Nymania capensis* $2n =$ ca. 48 (Aitoniaceae); *Ilex pedunculosa* $2n = 120$ (Aquifoliaceae); *Oroxylon indicum* $2n = 38$, *Millingtonia hortensis* $2n = 30$ (Bignoniaceae); *Canella alba* $2n = 28$ (Canellaceae); *Cneorum tricoccum* $2n = 36$ (Cneoraceae); *Eucryphia lucida* $2n = 30$ (Eucryphiaceae); *Greyia sutherlandii* $2n = 32$–34, $n =$ ca. 17 (Greyiaceae); *Koeberlinia spinosa* $2n =$ ca. 88 (Koeberliniaceae); *Erythrina burttii* $2n =$ ca. 168 (Leguminosae); *Rhynchocalyx lawsonioides* $2n = 20$ (Lythraceae); *Montinia carylophyllacea* $n = 34$, $2n = 68$ (Montiniaceae); *Olinia emarginata* $2n =$ ca. $40(-42)$, *O. radiata* $n =$ ca. $30(-28)$ (Oliniaceae); *Oftia africana* $2n = 38$, $n =$ ca. 19 (Scrophulariaceae).

A survey of cytology and evolution in the Angiosperms by Raven (1975) has brought to attention many examples of groups that are unknown cytologically. Numerous gaps exist both at the family level and amongst phylogenetically critical subfamilies and genera. The present paper, in which the cytology of several rare or critical taxa is reported, represents a contribution to our knowledge of some of these groups.

Of the 22 collections, representing 18 taxa studied here, 11 are believed to be the first reports for the following families: Montiniaceae and Oliniaceae, and if the following are recognized, Aextoxicaceae, Aitoniaceae, Eucryphiaceae, Greyiaceae, Koeberliniaceae and Oftiaceae. In addition to the genera in these families (*Montinia*, *Olinia*, *Aextoxicon*, *Nymania*, *Eucryphia*, *Greyia*, *Koeberlinia*, and *Oftia*), the present report also includes first records for the following genera: *Canella* (Canellaceae), *Gethyum* (Alliaceae), and *Rhynchocalyx* (Lythraceae). Previous reports for *Cneorum* (Cneoraceae), *Oroxylon*, and *Millingtonia* (Bignoniaceae) are substantiated while high polyploidy in species of *Ilex* (Aquifoliaceae) and *Erythrina* (Leguminosae) is confirmed.

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[2] Counts for *Olinia radiata*, *Oftia africana* and *Greyia sutherlandii* were made by A. M. Powell, Department of Botany, Sul Ross University, Alpine, Texas.

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I. MONOCOTYLEDONS

ALLIACEAE

Miersia chilensis Lindl. $2n = 20$. CHILE. PROV. VALPARAÍSO: El Granizo above Olmué, *Stebbins and Fry s.n.* (cult. MBG, *Goldblatt 3407* [MO]).

Gethyum atropurpureum Phill. $2n = 14$. CHILE. PROV. SANTIAGO: Quebrada Peñalolén, above Las Aguilas, 1,000 m, *Stebbins & Zeiger* 8885 (cult. MBG, *Goldblatt 3406* [MO]).

Gethyum atropurpureum. $2n = 14$. CHILE. PROV. SANTIAGO: Quebrada Peñalolén, 1,100 m, *Stebbins & Zeiger 8884* (cult. MBG, *Goldblatt 3402* [MO]).

The cytology of only one species in the distinctive South American tribe Gilliesieae has previously been described. Cave & Bradley (1943) reported *Miersia chilensis* as having diploid numbers of $2n = 20$ and 21. An investigation of the same species of *Miersia*, reported here as $2n = 20$, confirms the characteristics reported by Cave & Bradley: the chromosomes are very large and either telocentric or more or less metacentric. The diploid number of $2n = 14$ in *Gethyum atropurpureum* is a first report for this genus.

The karyotype of *Miersia chilensis* consists of 9 telocentric and 1 metacentric chromosome pairs (9T + 1M). The karyotype of *Gethyum* has exactly the same number of chromosome arms, but they are arranged as follows: 3 telocentric and 4 metacentric pairs (3T + 4M). The relationship between the karyotypes of the two species is clearly Robertsonian, the telocentrics either having fused to form metacentrics, or the metacentrics may have broken up to produce the telocentrics. The direction of chromosome change in these two closely related representatives of the Gilliesieae is likely to have been towards chromosome fusion and a decrease in number since *Gethyum* is clearly a more specialized genus than *Miersia*, *Gethyum* having only three anthers in contrast with the six in *Miersia*.

The tribe Gilliesieae is here assigned to Alliaceae following Airy Shaw (1973), and the very large chromosomes found accord with this treatment, though large chromosomes are also found in related families such as Amaryllidaceae and many genera of Liliaceae. With so few counts for Gilliesieae, a tribe of several genera, it is not possible to suggest a basic chromosome number for the alliance. Clearly, in view of the chromosomal variation already discovered, further study of the group will be rewarding.

II. DICOTYLEDONS

AEXTOXICACEAE

Aextoxicon punctatum Ruiz & Pavón. $2n = 32$. CHILE. PROV. VALDIVIA: Isla Teja, cult. MBG, *Goldblatt 3410* (MO).

The first chromosome count for this monotypic family from southern Chile, $2n = 32$, suggests a base number of either $x = 16$ or $x = 8$. The family is usually associated either with Euphorbiales or Celastrales in both of which are recorded

a wide range of chromosome numbers. Chromosome number alone thus seems of little help in establishing the relationship of Aextoxicaceae.

AITONIACEAE (MELIACEAE)

Nymania capensis (Thunb.) S. O. Lindb. $2n = ca.\ 48$. SOUTH AFRICA. CAPE: Little Karoo near Ladismith, *Goldblatt 1695* (MO).

Though it is usually referred to Meliaceae, the true affinities of *Nymania* are uncertain. The genus has been placed in its own family, Aitoniaceae, perhaps preferable in view of its peculiarities. The high base number, perhaps $x = 12$, is consistent with placement within Sapindales, but does not exclude alternative treatment. A point worth recording about *Nymania* is that seedlings grown for this study produced deeply trilobed leaves dotted with chalk glands, features evidently unrecorded, as *Nymania* is generally regarded as having simple and entire lanceolate leaves.

AQUIFOLIACEAE

Ilex pedunculosa Miq. $2n = 120$. Plants obtained from Bond Hartline Nursery Route 1, Anna, Ill., wild source not known, cult. MBG, *Goldblatt 3403* (MO).

The present count contradicts the earlier report of $2n = 110$ (Frierson, 1959), though it does confirm the polyploid nature of *Ilex pedunculosa*. The basic chromosome number in *Ilex* is $x = 20$, making this species hexaploid. The previous report of $2n = 110$ must be viewed with misgiving in this light. The present count confirms the presence of polyploidy in this genus, all other species being diploid, $n = 40$.

BIGNONIACEAE

Oroxylon indicum Vent. $2n = 38$. Seeds from University of Florida. Food and Agricultural Sciences Institute, Homestead, Florida, wild source unknown, cult. MBG, *Goldblatt 3410* (MO).

Millingtonia hortensis L.f. $2n = 30$. Seeds from Prachi Gobeson (Seed Co.) Belgharia, Calcutta, India, wild source unknown, cult. MBG, *Goldblatt 3408* (MO).

Counts for these two reputedly primitive genera of Bignoniaceae confirm earlier published records. With $2n = 28$ reported for the third time (Ghatak, 1956; Mangenot & Mangenot, 1962) in *Oroxylon indicum*, an early record of $2n = 30$ (Venkatasubban, 1944 fide Federov, 1969) must be viewed with misgiving.

These numbers, $n = 14$ and 15, both for Old World, reputedly primitive genera, contrast strongly with $n = 20$, by far the most common number in Bignoniaceae, which is found in all tribes. The record for *Oroxylon*, $n = 14$, is particularly significant as it belongs to the small group of Bignoniaceae with five stamens. Taken together with the frequent occurrence of $n = 20$, the record for *Oroxylon* strongly suggests $x = 7$ as basic in Bignoniaceae as noted by Raven (1975) with the hexaploid condition predominating in the family.

CANELLACEAE

Canella alba Murr. $2n = 28$. Seed obtained from wild plants near Homestead, southern Florida, cult. MBG, no voucher.

The only previous count in Canellaceae is a report of $2n = 26$ in *Capsicodendron* (Occhioni, 1945). The number reported here for *Canella alba* indicates that it also is tetraploid. Further studies in the family are needed before the significance of the two recorded chromosome numbers can be evaluated.

CNEORACEAE

Cneorum tricoccum L. $2n = 36$. SPAIN. Seeds from Barcelona Botanic Garden, wild source not given, *Goldblatt 3404* (MO).

The number reported here confirms the previous count of $2n = 36$ (Kliphuis & Weberling, 1972) for this species.

EUCRYPHIACEAE

Eucryphia lucida (Labill.) Baill. $2n = 30$. AUSTRALIA. TASMANIA: West Coast mountains near Queenstown, *Ratkowsky 16* (MO).

The first report for this small monogeneric family suggests a possible base number of $x = 15$. The affinities of Eucryphiaceae lie with the Saxifragales (Rosales) in which low base numbers are characteristic. Further counts in *Eucryphia* are needed to establish whether polyploidy is fundamental in the family.

GREYIACEAE

Greyia sutherlandii Hook. & Harv. $n =$ ca. 17.[4] SOUTH AFRICA. TRANSVAAL: Graskop, *Raven 26107* (MO).

Greyia sutherlandii. $2n = 32$–34. SOUTH AFRICA. Exact locality unknown, ex Hort. Kirstenbosch, cult. MBG, *Goldblatt 3409* (MO).

The two counts described here are first reports for *Greyia*, a genus usually assigned to Sapindales, either as Greyiaceae or Melianthaceae. Hutchinson (1967), however, believes the genus misplaced here, and allies *Greyia* (as Greyiaceae) to Cunoniales, close to Escalloniaceae. The high base number, $x = 16$ or 17, indicated here, would be consistent with either treatment.

KOEBERLINIACEAE

Koeberlinia spinosa Zucc. $2n =$ ca. 88. UNITED STATES. NEW MEXICO: Near Rodeo, *Roth s.n.* (no voucher).

The report here of $2n =$ ca. 88 for the monotypic Koeberliniaceae must be regarded at this point as only tentative, though the count is as accurate as pos-

[4] Count made by A. M. Powell.

sible for mitotic material. The chromosomes are very small and can easily be overlooked when they overlap one another.

LEGUMINOSAE

Erythrina burttii Baker f. $2n =$ ca. 168. KENYA. Between Kajiado and Bissel, *Ng'weno s.n.* (EAH-15822).

An earlier count for *Erythrina burttii*, $2n =$ ca. 126 (Atchison, 1951) indicated this species may be hexaploid ($x = 21$ in *Erythrina*). While the present count confirms the polyploid nature of *E. burttii*, material at hand is octoploid, $2n =$ ca. 168 representing the highest number reported in the genus (Lewis, 1974). Before the significance of the differences in ploidy can be evaluated, further material needs to be examined, but it should be noted that Atchison's hexaploid material was of Tanzanian origin, while the octoploid reported here is from Kenya.

LYTHRACEAE

Rhynchocalyx lawsonioides Oliv. $2n = 20$. SOUTH AFRICA. NATAL: Port Shepstone district, *Strey s.n.* (MO).

Rhynchocalyx, the monotypic South African genus (Strey & Leistner, 1968) usually assigned to Lythraceae, has more recently (van Beusekom-Osinga & van Beusekom, 1975) been placed in Crypteroniaceae, also in the Myrtales. A base number of $x = 8$ seems indicated for Lythraceae (Raven, 1975) but $x = 10$ does occur in a few genera: *Lafoensia* ($n =$ ca. 10) and *Nesaea* ($n = 30$). No chromosome numbers have been reported for other genera assigned to Crypteroniaceae. The number recorded here for the very rare *R. lawsonioides*, $2n = 20$ is thus not as yet of value in determining its family relationships.

MONTINIACEAE

Montinia caryophyllacea Thunb. $n = 34$. SOUTH AFRICA. CAPE: Kirstenbosch Gardens, Cape Peninsula, *Goldblatt 3500* (MO).

Montinia caryophyllacea. $2n = 68$. SOUTH AFRICA. CAPE: Bains Kloof, *Goldblatt 1353* (MO).

This, the first cytological report for the monotypic *Montinia*, recently placed with *Grevea* in Montiniaceae (Milne-Redhead, 1955), indicates a base number of $x = 17$. Montinia has in the past generally been assigned to Saxifragaceae but its affinities are not clear. Milne-Redhead has suggested that Montiniaceae may be most closely related to the African Oliniaceae, but the reports (below) of $x =$ ca. 20 in *Olinia* provide no support for this treatment. It is perhaps worth mentioning that Dahlgren (1975) tentatively includes Montiniaceae in Celastrales. Raven (1975) suggested a base number of $x = 12$ for this order, with important, early aneuploidy. Higher base numbers are encountered in Aquifoliaceae ($x = 20$), Hippocrateaceae ($x = 14$), while in Celastraceae for example, $x = 16$ in *Euonymus* and $x = 23$ in *Celastrus*.

OLINIACEAE

Olinia emarginata Burtt-Davy. $2n$ = ca. 40(–42). SOUTH AFRICA. Cult. at Kirstenbosch Botanic Garden, original locality unknown, *Goldblatt 1466* (MO).
Olinia radiata J. Hoffm. & Phill. n = ca. 30(–28).[5] SOUTH AFRICA. NATAL: Ngoya Forest, *Raven 26126* (MO).

The monogeneric Oliniaceae is a peculiar African family, believed to belong to Myrtales. The base number of $x = 10$, likely on the basis of these counts, fits in well with other numbers for the order, in which $x = 12$ (or 11) is probably basic (Raven, 1975). The presence of polyploidy in the *Olinia* is also indicated, and further investigations are clearly needed to confirm the numbers reported here and to establish the base number more firmly.

SCROPHULARIACEAE

Oftia africana (L.) Bocq. $2n = 38$. SOUTH AFRICA. CAPE: Kirstenbosch, foot of Window Gorge, cult. MBG, *Goldblatt 3405* (MO).
Oftia africana. n = ca. 19.[5] SOUTH AFRICA. CAPE: Hermanus, *Raven 26155* (MO).

The genus *Oftia*, comprising three species of shrubby plants, occurs in the Cape region of southern Africa. The affinities of *Oftia* were for a considerable time believed to be with the Myoporaceae (Rolfe, 1912; Melchior, 1964; Hutchinson, 1959). The Myoporaceae (with a base number of $x = 9$) are predominantly Australasian in distribution with an outlier in the West Indies, and the placement of *Oftia* in this comparatively advanced and specialized family seems improbable. More recently Takhtajan (1969) has noted that *Oftia* is isolated within the Myoporaceae. Dahlgren & Rao (1971) present an array of evidence showing *Oftia* to be considerably more closely allied to *Teedia* (Scrophulariaceae), a southern African genus, than to Myoporaceae. Dahlgren & Rao conclude that it is subjective whether to regard *Oftia* as a distinct family or as a member of the Scrophulariaceae since it has several unusual features, although generally agreeing with *Teedia*. Chromosome studies in the Scrophulariaceae, summarized by Raven (1975), indicate that the base number in the family may be $x = 7$, but other numbers such as $x = 8$, 9, and 10 are common. *Oftia* falls within this range at the tetraploid level, and although $n = 19$ has not previously been recorded in the family, none of the several woody African representatives of Scrophulariaceae, to which *Oftia* may be allied, are known cytologically.

LITERATURE CITED

AIRY SHAW, H. K. 1973. J. C. Willis. A Dictionary of the Flowering Plants and Ferns. Ed. 8. University Press, Cambridge.
ATCHISON, E. 1951. Studies in the Leguminosae. VI. Chromosome number among tropical woody species. Amer. J. Bot. 38: 538–547.
BEUSEKOM-OSINGA, R. J. VAN & C. F. VAN BEUSEKOM. 1975. Delimitation and subdivision of the Crypteroniaceae (Myrtales). Blumea 22: 255–266.
CAVE, M. S. & M. V. BRADLEY. 1943. Alteration of chromosome number in *Miersia chilensis*. Amer. J. Bot. 30: 142–149.

[5] Count made by A. M. Powell.

DAHLGREN, R. 1975. A system of classification of the Angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119–147

——— & V. S. RAO. 1971. The genus *Oftia* Adans. and its systematic position. Bot. Not. 124: 451–472.

FEDEROV, A. (editor). 1969. Chromosome Numbers of Flowering Plants. V. L. Komarov Botanical Institute, Leningrad.

FRIERSON, J. L. 1959. Cytotaxonomic study of selected indigenous and introduced species of the genus *Ilex*, commonly grown in the United States. Ph.D. dissertation. Univ. South Carolina.

GHATAK, J. 1956. A contribution to the life-history of *Oroxylon indicum* Vent. Proc. Indian Acad. Sci., Sect. B 43: 72–87.

HUTCHINSON, J. 1959. The Families of Flowering Plants. Vol. 1. Dicotyledons. Ed. 2. Clarendon Press, Oxford.

———. 1967. The Genera of Flowering Plants. Vol. 2. Clarendon Press, Oxford.

KLIPHUIS, E. & J. H. WEBERLING. 1972. Chromosome numbers of some Angiosperms from the south of France. Acta Bot. Neerl. 21: 598–604.

LEWIS, W. H. 1974. Chromosomes and phylogeny of *Erythrina* (Fabaceae). Lloydia 37: 460–464.

MANGENOT, S. & G. MANGENOT. 1962. Enquête sur les nombres chromosomiques dans une collection d'espèces tropicàles. Rev. Cytol. Biol. Vég. 25: 411–447.

MELCHIOR, E. (editor). 1964. A. Engler's Syllalus der Pfanzenfamilien. Ed. 12. 2 vols. Gebrüder Borntträger, Berlin.

MILNE-REDHEAD, E. 1955. Montiniaceae. Hooker's Icon. Pl.: *Tab. 3541–3544.*

OCCHIONI, P. 1945. Contribuicao para o conhecimento da flora do distrito federal. Rodrigúesia 9: 57–65.

RAVEN, P. H. 1975. The bases of angiosperm phylogeny: Cytology. Ann. Missouri Bot. Gard. 62: 724–764.

ROLFE, R. A. 1912. Myoporaceae. *In* W. T. Thiselton-Dyer (editor), Flora Capensis. Vol. 5: 92–94.

STREY, R. G. & O. A. LEISTNER. 1968. The rediscovery of *Rhyncocalyx lawsonioides* Oliv. J. S. African Bot. 34: 9–13.

TAKHTAJAN, A. 1969. Flowering Plants: Origin and Dispersal. Transl. by C. Jeffrey. Oliver & Boyd, Edinburgh.

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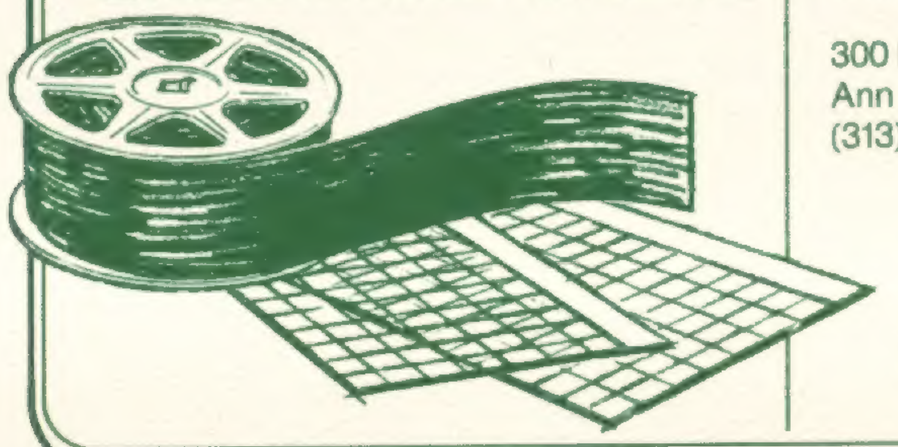

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